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EXPERIMENTAL STUDIES ON SPECIES RELATIONSHIPS IN *CEANOTHUS*

Malcolm A. Nobs

Carnegie Institution of Washington Publication 623
Washington, D. C.
1963

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PREFACE

The effectiveness of experimental studies directed specifically toward improving our understanding of relationships between and within species of plants, and of basic evolutionary mechanisms, is now widely recognized. This recognition has been won through the efforts of groups of investigators in a relatively few research centers in various countries of the world during the last forty years.

The present study of *Ceanothus* is the product of extensive investigation while the author was a graduate student in the Department of Botany at the University of California at Berkeley and later as a staff member at the Department of Plant Biology of the Carnegie Institution at Stanford University. Begun in 1940, this study was interrupted during World War II by service in the armed forces. It represents a departure in the experimental work on plant relationships in that it ventures into the problem of dealing with a genus of slow-growing, woody shrubs and low trees that contribute heavily to the over-all ground cover of large foothill and mountain areas in the far western states. The techniques developed for faster-growing herbaceous species that have hitherto been used almost exclusively in experimental studies can be applied only to a limited extent in such a shrubby group.

In the present work emphasis has been placed on field observations supplemented by intensive laboratory studies in anatomy, cytology, and crossing experiments. The extensive data, examined in the light of the past and present ecological distribution of the recognizable taxa of this variable genus of the buckthorn family, lead to a dynamic picture of the evolution of the various components of *Ceanothus* and their current status in a world of changing environments.

ACKNOWLEDGMENTS

It is a pleasure to thank the many persons who have aided the author during the course of this study. He is especially indebted to Professor H. L. Mason of the Department of Botany at the University of California for his continued interest and encouragement, and for making available his living collections of *Ceanothus* for genetic study; and to Professors G. L. Stebbins and Lincoln Constance for their advice and criticism.

The late Professor Milo S. Baker of the Santa Rosa Junior College made both his personal collections of *Ceanothus* and his intimate field knowledge of the principal study area freely available. Professor Howard E. McMinn of Mills College, Oakland, gave the author access to his herbarium collections and his living cultures of *C. masonii*. Likewise Mr. James Roof, director of the Botanic Garden of the East Bay Regional Park District in Charles Lee Tilden Regional Park, and Mr. Louis L. Edmonds of Danville, California, granted extensive use of their collections of *Ceanothus* for cytological, genetic, and anatomical study.

The curators of many herbaria have supplied facilities for study at their respective institutions. Professor T. Harper Goodspeed made available the facilities of the Botanic Garden at the University of California for the culture of the experimental populations. Dr. Lee W. Lenz furnished information on experimental F_2 hybrid cultures grown at the Ranch Santa Ana Botanical Garden at Claremont, California, and Dr. Rafael Rodríguez, formerly at Berkeley and now at the University of Costa Rica, helped in the study of the vascular anatomy of the *Ceanothus* flower. The staff of the Carnegie Institution of Washington Department of Plant Biology at Stanford have freely provided garden facilities for the culture of second-generation hybrids and made critical suggestions in the preparation of this manuscript.

Among many individuals who have generously contributed field collections and other material are Miss Annetta Carter, Dr. Lincoln Constance, Drs. Vern and Alva Grant, Dr. Arthur R. Kruckeberg, Dr. Calvin McMillan, Dr. Reed Moran, Mr. C. R. Quick, Dr. Jack Rattenberry, Dr. Peter (Kamb) Ray, Mr. Clifton F. Smith, Dr. S. Galen Smith, Dr. G. L. Stebbins, and Dr. James R. Sweeney.

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CHAPTER I

COMPOSITION, DISTRIBUTION, AND CRITICAL CHARACTERS IN CEANOTHUS

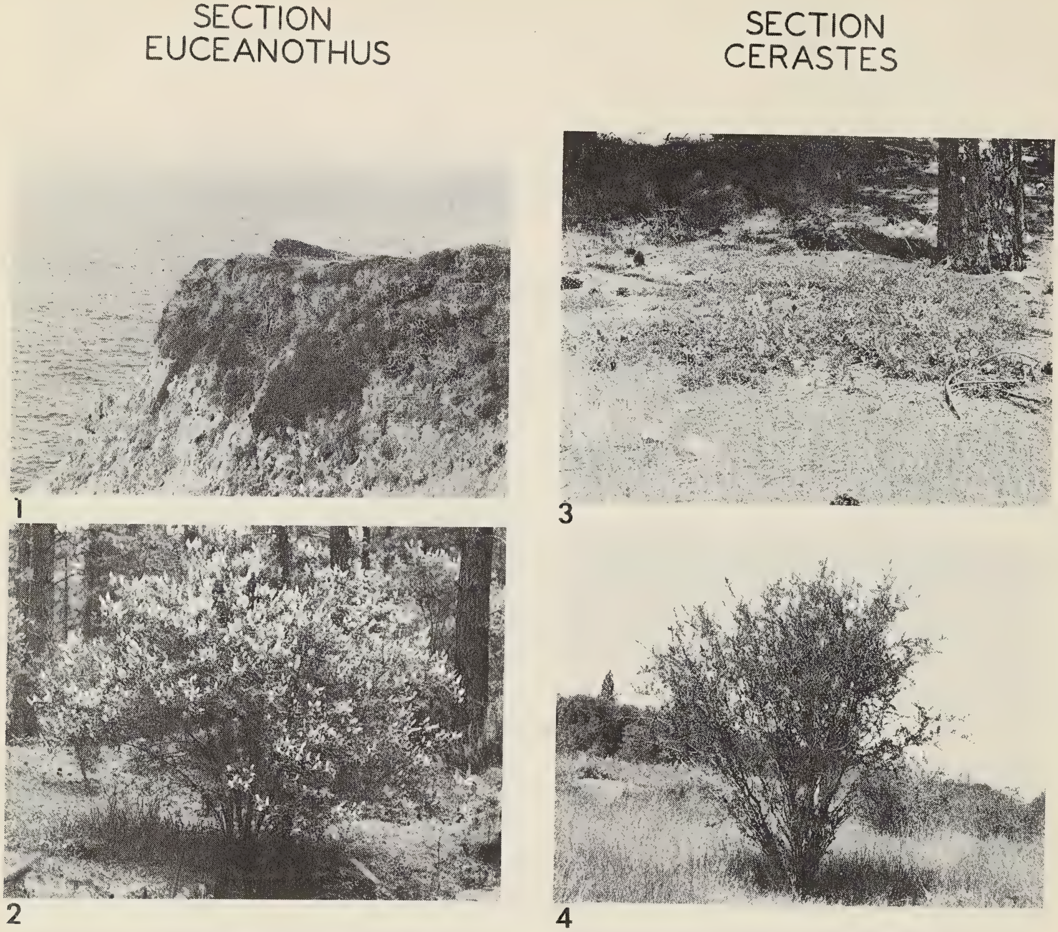
Introduction

Ceanothus, the mountain lilac, is a genus of shrubs or small trees in the buckthorn family (Rhamnaceae) composed of approximately 55 species (McMinn, 1942). All are native to North America, and are distributed from Guatemala (ca. lat. 16°N) northward into southern Canada (ca. lat. 55°N) and from the Pacific coast east to the Atlantic. Most of the species are limited to the Pacific coast, 44 being endemic to California.

The species are grouped into two natural sections, Euceanothus DC and Cerastes S. Wats. Within each section there are various kinds of species, ranging from narrowly restricted endemics to widely distributed polymorphic complexes, and members of the genus are found in habitats extending from coastal bluffs to subalpine conditions. The two sections are so well differentiated that they represent major evolutionary lines within the genus, as will become clear from evidence presented in later pages. Parallel variation among the members of the two sections is strikingly evident, as expressed, for example, in such characters as habit of growth, illustrated in figures 1 to 4.

The genus Ceanothus is well known from a descriptive point of view, for it has received a great deal of taxonomic attention since its original designation by Linnaeus in 1735. The major works dealing with the group are: De Candolle (1825), Torrey and Gray (1838), Watson (1875, 1876), Trelease (1888, 1897), Parry (1889a and b), K. Brandegee (1894), Standley (1923), McMinn (1930, 1939, 1942, 1944), Jepson (1936), Howell (1939a and b; 1940a, b, and c), Abrams (1951), and Sussenguth (1953).

One of the most interesting aspects of the genus is the apparent close relationship between the species within each section, evidenced both by overlapping morphological characters and the frequent occurrence of spontaneous hybrids between the taxa. The latter characteristic of the members of the genus was keenly appreciated by early workers: Trelease (1888) suggested the suitability of Ceanothus for the study of evolutionary stages in speciation, and Brandegee (1894) not only postulated a theory for the origin of the perplexing interlocking



Parallel growth forms in *Ceanothus*

Fig. 1. *Ceanothus thyrsiflorus* (Esch) var. *repens* McMinn: dense prostrate mats on coastal bluffs, Mendocino County, California. Fig. 2. *C. integerrimus* Hook. and Arn.: an erect understory shrub in *Pinus ponderosa* forests of the lower Sierra Nevada; Grass Valley, Nevada County, California. Fig. 3. *C. prostratus* Benth: prostrate ground cover in *Pinus ponderosa* forests; Grass Valley, Nevada County, California. Fig. 4. *C. cuneatus* (Hook.) Nutt.: chaparral shrub from the Sierran foothills; south of Bear River, Placer County, California.

species through hybridization and random survival but also described an experimental approach to test the theory through the artificial synthesis of these entities by hybridization. In recent years these evolutionary aspects of the genus have received considerable attention by Howell (1939a and b, 1940c) and McMinn (1942, 1944), although very few experimental data have been available.

The primary objective of the present work was to obtain factual information by experimental means to clarify biosystematic and evolutionary relationships in this genus that have heretofore been a matter of so much doubt and speculation. For this purpose the section *Cerastes*, containing twenty-two species, was selected for detailed study, with particular concentration on the cytogenetics, variation pattern, and ecology of eleven species that occur in a limited area of about 7500 square miles in the coast ranges north of San Francisco Bay. From these correlated studies a clear picture of the evolutionary pattern in these species becomes evident which is probably typical of the section *Cerastes* and the entire genus.

No taxonomic revision is being proposed here, since the monographic treatment of *Ceanothus* by McMinn (1942) adequately recognizes essentially all the known taxa. Although minor revisions might be suggested in the light of newer data, the nomenclature used by McMinn has been followed throughout.

Anatomical Studies

Because certain anatomical features of *Ceanothus* are of particular help in delimiting the major sections of the genus, in distinguishing between species, and in detecting spontaneous interspecific hybrids and their derivatives in wild populations, considerable study has been devoted to them. One feature is the structure of the flowers, which, although remarkably constant in the genus and even in the entire family Rhamnaceae to which it belongs, deviates in the single species *Ceanothus jepsonii* Greene, which has a perianth of six to eight segments as compared with the five segments found in the other members of the genus. This character in *C. jepsonii* has been useful as a marker in evaluating the amount of genetic exchange that has taken place between this species and others at their points of contact.

A second feature, one of even more importance, is the structure of the leaves. In section *Cerastes* the leaves have stomatal crypts on their lower surfaces. The structure of the crypts and the nature and distribution of their associated tomentum provide characters that not only serve to identify the species but also give important clues about the evolutionary history of members of the section.

The following paragraphs will present the anatomical evidence to which reference will be made in subsequent chapters.

Materials and Techniques

The materials for the studies of leaf and floral anatomy were obtained from field collections and from specimens in the University of California Herbarium, Berkeley.

Leaf collections were fixed in the field in a solution of formalin, propionic acid, and alcohol (FPA of Sass, 1940, p. 16) and brought to the laboratory, where they were sectioned by hand. The sections were stained in Safranin (1 per cent solution in 50 per cent ethyl alcohol), dehydrated, counterstained in Fast Green

(1 per cent solution in clove oil), and mounted in Euparal. Material from herbarium specimens was first softened in an aqueous solution of detergent, aspirated under partial vacuum, transferred to 70 per cent alcohol, and then prepared as above.

In addition, cleared whole leaves and transections 0.2 to 0.5 mm thick were prepared. Leaves and sections were first leached in 5 per cent sodium hydroxide until they showed signs of clearing, a time interval of 2 to 5 days. They were then transferred into Stockwell's chrome-acetic bleach (Johansen, 1940, p. 85) for 8 to 10 hours to remove tannins. If the leaves remained opaque after treatment, they were washed in water and transferred to lactic acid until cleared. They were then stained in aniline blue in 95 per cent alcohol, dehydrated, and mounted in Euparal. By means of this clearing method the entire crypt as well as the venation pattern of the leaf could be studied.

Floral Structure

The study of floral anatomy was limited to the vascular system in flowers of Ceanothus jepsonii, C. cuneatus, C. gloriosus (Cerastes), C. arboreus, and C. thyrsiflorus (Euceanothus), all taken at anthesis. The flowers were prepared by clearing in the same manner as described above for the leaf. From this study a comparative picture of the vascular pattern of C. jepsonii and two members each of sections Cerastes and Euceanothus was obtained at this stage of development.

Ceanothus jepsonii Greene has a hexamerous to octamerous arrangement in the perianth and androecium, rather than the pentamerous structure common to all the other species of Ceanothus. This species is unique likewise in the family Rhamnaceae and even in the entire order of Rhamnales, there being only one other genus, Colletia, of the Rhamnaceae, which is reported to have occasional hexamerous flowers in some species rather than the tetramerous to pentamerous condition common to the order (Sussenguth, 1953).

There seems to be no doubt that the specimen upon which Greene (1894) based his original description of C. jepsonii had hexamerous flowers. Although no type was designated, all material of this species represented in the Greene-Nieuwland Herbarium (including the specimen from San Geronimo Ridge, Marin County, the type locality, collected before 1894) has six sepals, six petals, and six stamens (Dr. A. L. Delisle, Curator, Greene-Nieuwland Herbarium, personal correspondence). The same is true of all flowering material represented in the Jepson Herbarium at the University of California, Berkeley. The number of the perianth parts found in fourteen population samples taken from different localities throughout the range of this species is summarized in table 1. It is apparent that, although some plants in a typical population have occasional pentamerous flowers, the larger number of segments is highly characteristic of this species.

The floral structure is basically the same in all species of Ceanothus. The flowers are perigynous with a moderately well developed hypanthium (fig. 5). The colored sepals are valvate and alternate with the clawed petals. The stamens

TABLE 1. Variation in Floral Structure among 14 Natural Populations of *Ceanothus jepsonii*

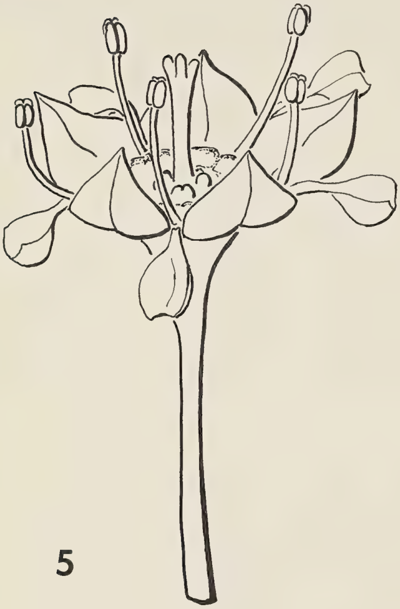
Origin and Collection No.	5- to 6-merous	6- to 7-merous	7- to 8-merous	Total
San Geronimo Ridge, Marin Co. (400)	1	31	0	32
Mirabel Mine, Lake Co. (431)	2	27	2	31
Knoxville, Napa Co. (435)	1	34	8	43
B M 2012, Napa Co. (436)	0	27	8	35
B M 2029, Napa Co. (437)	1	18	6	25
McKosker Ranch, Lake Co. (438)	0	38	11	49
Colusa Lake Co. Line, Highway 120 (439)	0	18	17	35
Wilbur Springs, Colusa Co. (440)	0	14	9	23
Mt. Tamalpais, Marin Co. (500)	2	46	1	49
Table Mt., Lake Co. (561)	2	15	7	24
White Pt., Lake Co. (563)	0	30	1	31
Mt. Tamalpais, Marin Co. (629)	2	35	12	49
Alpine Dam, Marin Co. (631)	0	21	1	22
Skaggs Springs, Sonoma Co. (633)	2	25	3	30
Total	13	379	86	478

are opposite the petals and are of the same number; they arise from the inner surface of the hypanthium adjacent to a fleshy disc, which surrounds the trilocular ovary. Placentation is basal, and each locule of the ovary bears a single anatropous ovule.

The vascular pattern of the flowers of *C. cuneatus*, typical of all the species studied, is represented in the schematic diagrams figures 6 and 7. *Ceanothus jepsonii* deviates from this pattern only in that for each additional segment, including the sepal with its adjoining petal and stamen, one additional vascular bundle is found in the pedicel, which contributes the same series of vascular traces to the floral parts.

This unique condition in perianth and androecium is associated with an increase in flower size from a calyx diameter of 1-3 mm, as in other species, to 4-5 mm in *C. jepsonii*. Also linked with large flower size is a reduction in size and complexity of the inflorescence. In all species of the *Cerastes* section of *Ceanothus* except *C. jepsonii* there are three flowers at each node; in this species only one larger flower is present.

The increased size and number of floral parts in *C. jepsonii* appears to have been derived from the smaller-flowered pentamerous pattern common to the remainder of the genus. The reduction from three flowers per node to one suggests an increase in the size of the floral primordium that could result in larger flowers and an increase in the number of members in the perianth and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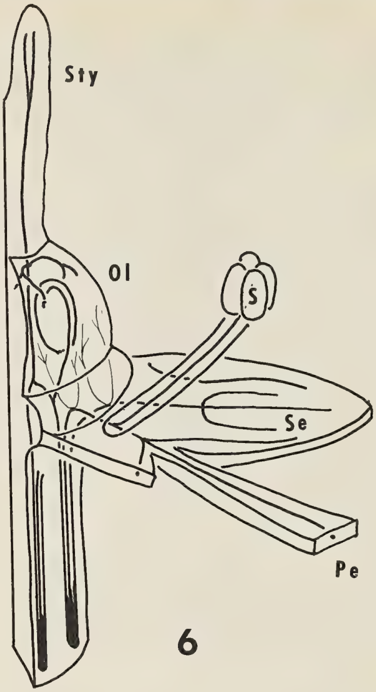

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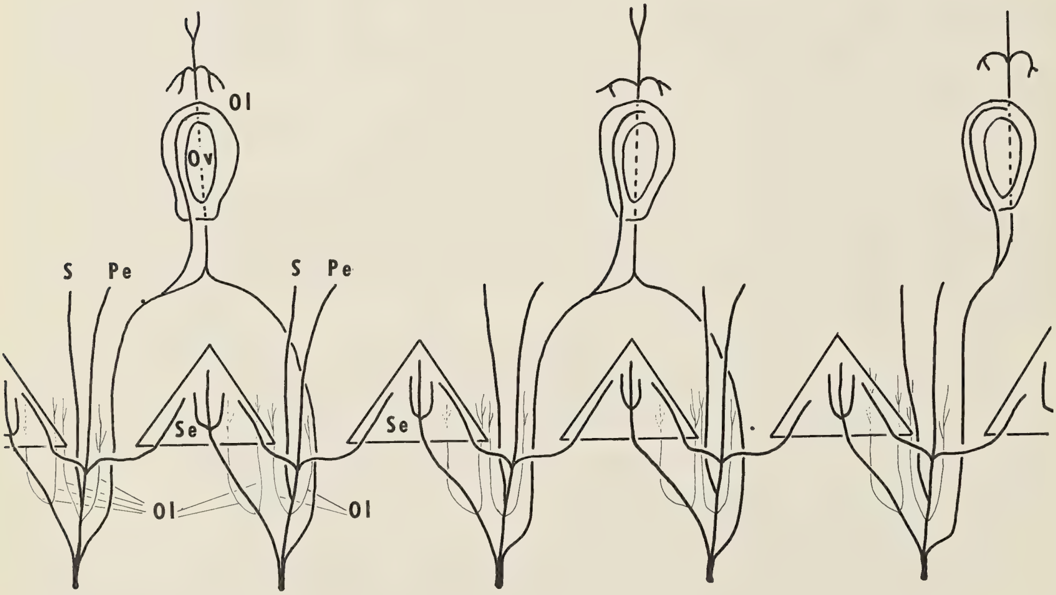

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Figs. 5-7. Floral structure and schematic representation of the vascular system of the flower of Ceanothus cuneatus. Sty, style; Ol, ovarian locule; S, stamen; Se, sepal; Pe, petal; Ov, ovule.

androecium. A comparable relationship is found in large-fruited tomatoes, where larger fruit size and increased number of locules are correlated with a larger size in the ovary primordium (Sinnott and Dunn, 1935; Houghtaling, 1935).

The number of perianth segments is genetically controlled. In hybrid combinations between *C. jepsonii* and seven other species, all F_1 plants have a mixed intermediate condition with about equal numbers of pentamerous and hexamerous flowers. In this respect it has been a useful character for estimating the extent of genetic exchange between *C. jepsonii* and species that occur sympatrically with it.

Leaf Anatomy

The organization of the petiole is uniform throughout the genus. Three traces, which arise from a trilacunar node, enter the base of the leaf axis and immediately fuse to form a single collateral bundle extending throughout the length of the petiole. The gross venation pattern of the lamina is uniformly pinnate in section *Cerastes*. In the *Euceanothus* section, however, both a trinerved and a strictly pinnate pattern are found, although the trinerved condition predominates and is probably basic. In both sections the secondary veins branch into a reticulate pattern of tertiary veinlets. These send off quaternary branches that enter the uppermost layer of the spongy parenchyma and end in a small cluster of storage tracheids.

The tissues of the lamina of the leaf have the same basic organization in both taxonomic sections. The epidermis of the adaxial surface of the leaf is uniserrate to partially and irregularly biserrate and is covered by a thick cuticle. Its cells are slightly elongate vertically and have straight walls thickened on the adaxial side. The epidermis of the abaxial surface is uniserrate, and in *Euceanothus* it is covered by a thick cuticle. In *Cerastes* the cuticle is limited to the exposed areas covering the vein extensions, and the cells are tabular with more or less undulating walls. In both sections the stomata, which are of the ranunculaceous type, are confined to the abaxial surface in the areas immediately adjacent to the loose, spongy parenchyma. The guard cells protrude more or less above the epidermis in a somewhat liplike manner, the extreme expression of this condition being found in *Cerastes*. Tanniferous substances are found in the cells of both the upper and lower epidermis. Unicellular hairs occur to some extent on both surfaces in most species of the genus, but their greatest development is on the abaxial surface.

The leaf mesophyll is separated into many small compartments by strutlike bundle sheath extensions, which are present on all but the quaternary veinlets and extend from the adaxial epidermis to a biserrate hypodermal layer lying between the bundle-sheath extension and the abaxial epidermis. The parenchymatous cells of these vein extensions are elongated parallel to the vein and contain tanniferous substances. Idioblastic cells containing druses are often found in the mesophyll immediately adjacent to these cells.

The palisade parenchyma is composed of two or three cell layers on the adaxial side of the leaf. The spongy parenchyma in the abaxial portion is closely packed and palisade-like immediately adjacent to the vein extensions, but in the centers of the compartments formed by the "struts" it is loose and composed of cells which are lobed and, in extreme cases, somewhat stellate.[1]

The Crypts

The organization of the lamina is modified sufficiently in all members of *Cerastes* to serve as one of the most important characters separating this section from *Euceanothus* (Gemoll, 1902; Cooper, 1922; McMinn, 1930). This is illustrated in figures 8 and 9. The lower surface of the leaf in *Cerastes* is strongly invaginated between the bundle-sheath extensions, forming cavities, the stomatal crypts, which extend through the spongy parenchyma into the mesophyll to a depth of more than half the thickness of the leaf. The quaternary veinlets are adjusted to fit these invaginations and arch over the crypts, terminating in the lower layer of the palisade parenchyma.

The crypt is formed in the young leaves of the developing *Cerastes* seedling. In *C. cuneatus*, *C. gloriosus*, *C. purpureus*, and *C. rigidus* the first seven pairs of leaves exhibit a developmental sequence beginning with the basic organization found in *Euceanothus* and terminating with the essentially mature crypt types of *Cerastes* (figs. 10 to 13).

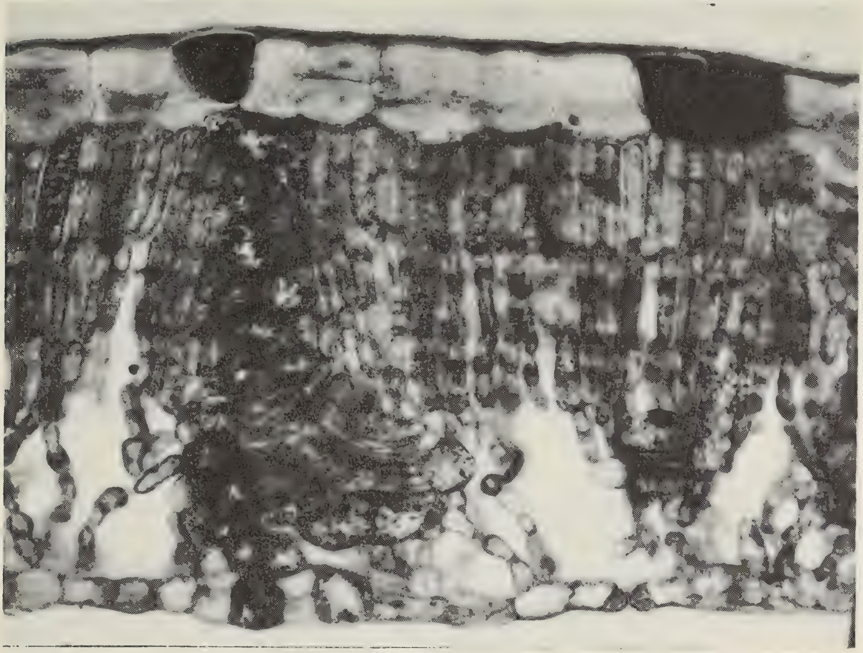
Mature plants in nature, with the exception of rare intersectional hybrids, do not exhibit forms intermediate between the cryptose leaves of *Cerastes* and the cryptless leaves of *Euceanothus*.

The crypts described above can be separated into three main types on the basis of the distribution of the associated unicellular hairs. For convenience, these will be designated types I, II, and III crypts, respectively. Type I has an abundance of kinky interlocking hairs distributed between the stomata over the entire inside surface of the crypt cavity (fig. 14). These hairs are densely packed, filling the entire crypt cavity. Type I crypts are characteristic of *C. insularis*, *C. verrucosus*, *C. megacarpus*, *C. rigidus*, *C. ferrisae*, and *C. jepsonii*. Type II differs from type I in that the unicellular hairs are restricted to the borders of the crypt aperture or to the epidermis covering the tips of the vein extensions, leaving the entire inner surface of the crypt glabrous (fig. 15). *Ceanothus crassifolius*, *C. confusus*, *C. divergens*, *C. gloriosus*, *C. pinetorum*, *C. prostratus*, *C. purpureus*, and *C. pumilus* have crypts exclusively of this type.

---

[1] Metcalfe and Chalk (1950) state that only palisade parenchyma is present in *Cerastes*. However, investigation of the lower leaf surface discloses that in this section the semistellate cells of this tissue are compressed together, giving the appearance of continuous palisade parenchyma.

EUCEANOTHUS **C. parryi**



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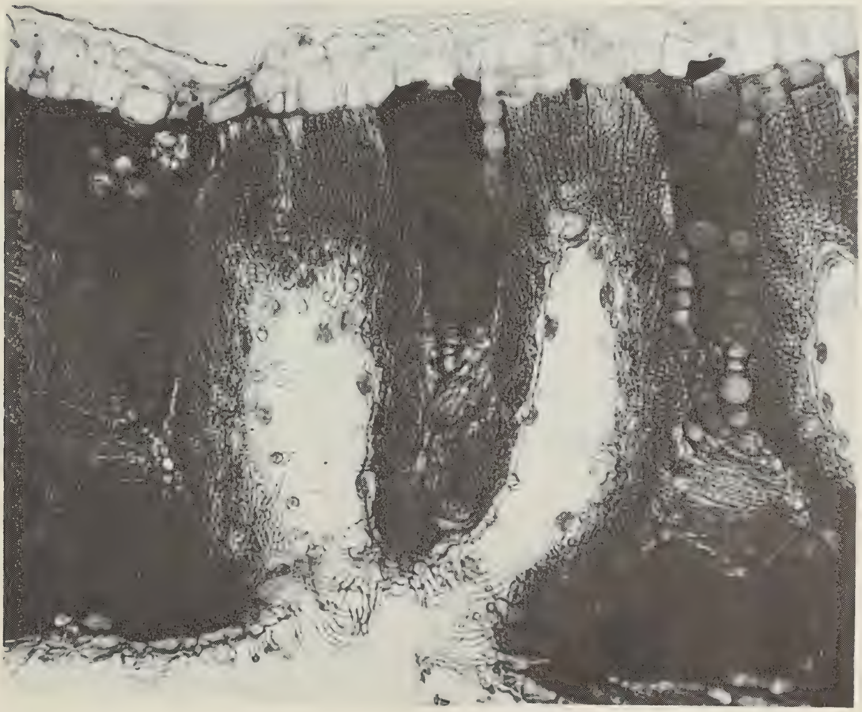
CERASTES **C. insularis**



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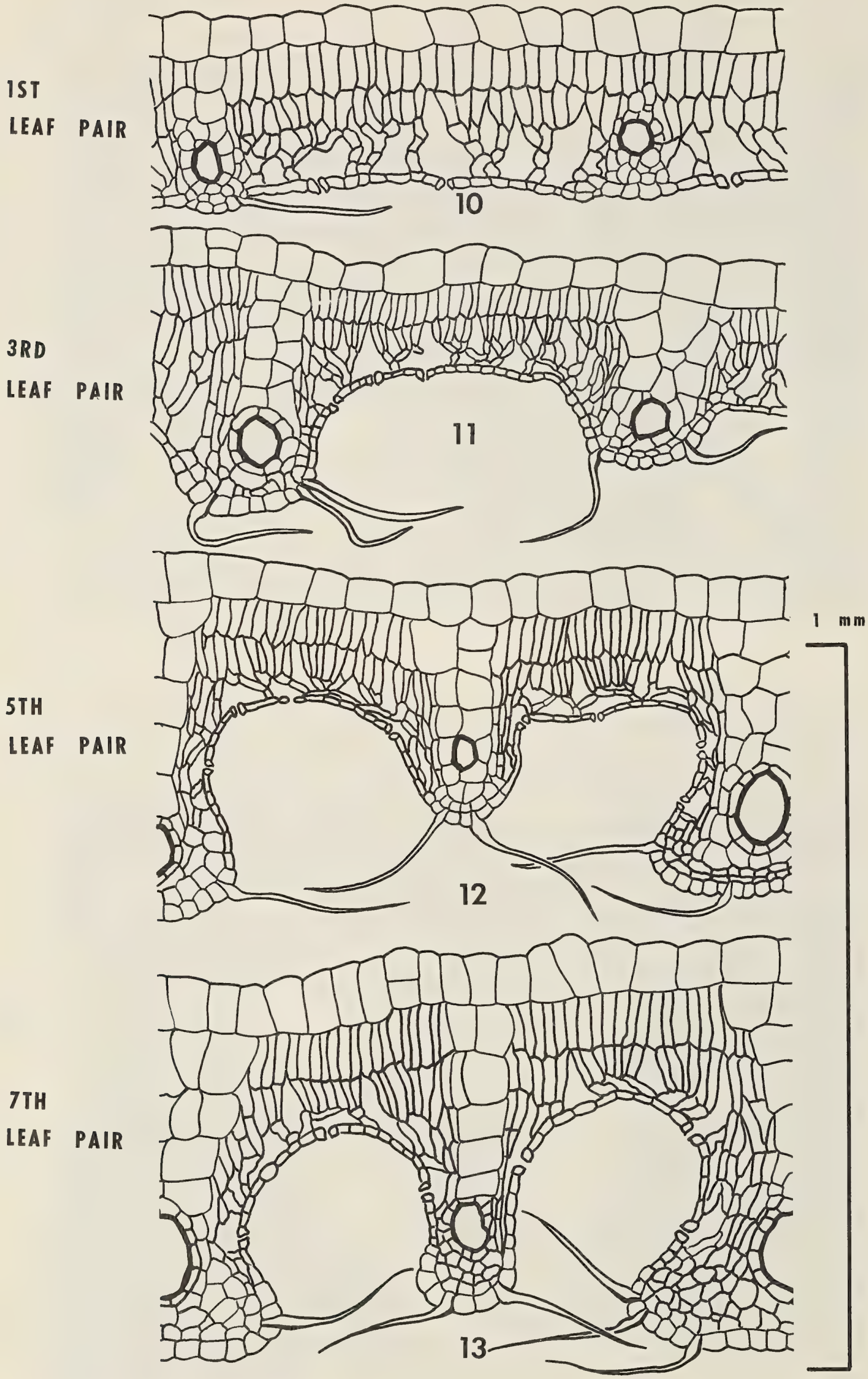
Figs. 8 and 9. Transections of *Ceanothus* leaves, showing structural differences between *Euceanothus* and *Cerastes*.



Figs. 10-13. Camera lucida drawings of transections of successive leaves of a seedling *Ceanothus gloriosus* plant, showing different degrees of crypt development.

Type III is intermediate between types I and II, with relatively few straight to undulating hairs which clothe the lower portion of the crypt wall to about two-thirds its depth, leaving the upper surface generally glabrous (fig. 16). Type III crypts are characteristic of *C. cuneatus*, *C. greggii*, and *C. lanuginosus*.

A group of highly variable taxa, which will be discussed in detail later, have crypts that vary from plant to plant within their populations. Without exception, these taxa are geographically situated in areas lying between the ranges of the above-mentioned groups of species. Examples include *Ceanothus arcuatus*, *C. fresnensis*, *C. ramulosus*, *C. masonii*, and *C. sonomensis*.

A description of the crypts with their associated trichomes as observed in the collection cited in each of the species of section *Cerastes* follows.

Type I crypts

insularis Eastw.

Crypts uniform; trichomes arising between stomata over the entire inner surface of crypt, kinky and interlocking, densely filling the entire crypt cavity (fig. 14).

Moran 3324, north of Canada Cervada, Santa Cruz Island; *R. Hoffman* (UC 675853), ridge south of Pelican Bay, Santa Cruz Island.

ferrisae McMinn

Description as in *C. insularis*.

Nobs 548-1 to *3*, north of Coyote Creek, 2.5 miles east of Highway 101, Madrone Springs Rd., Santa Clara Co.

jepsonii Greene

Description as in *C. insularis* (fig. 19).

Nobs 576-1 to *4*, Bootjack Camp, Mt. Tamalpais, Marin Co.; *Nobs 577-1* to *4*, St. Helena Creek at Napa-Lake Co. line, Highway 29, Lake Co.; *Nobs 674-1* & *2*, Gray Creek near fork of East Austin Creek, Sonoma Co.

megacarpus Nutt.

Description as in *C. insularis* (fig. 18).

C. F. Smith 2602, Santa Barbara Botanical Garden, Santa Barbara Co.; *Epling* (UC 440368), Mandeville Canyon, Santa Monica Mts., Los Angeles Co.

ramulosus var. *fascicularis* McMinn

Description as in *C. insularis*.

Nobs and *McMillan 670*, Sandy Plain 4 miles northeast of Lompoc, Santa Barbara Co.; *Kamb 1617-1* & *2*, west of Pozo Mt., San Luis Obispo Co.

rigidus Nutt.

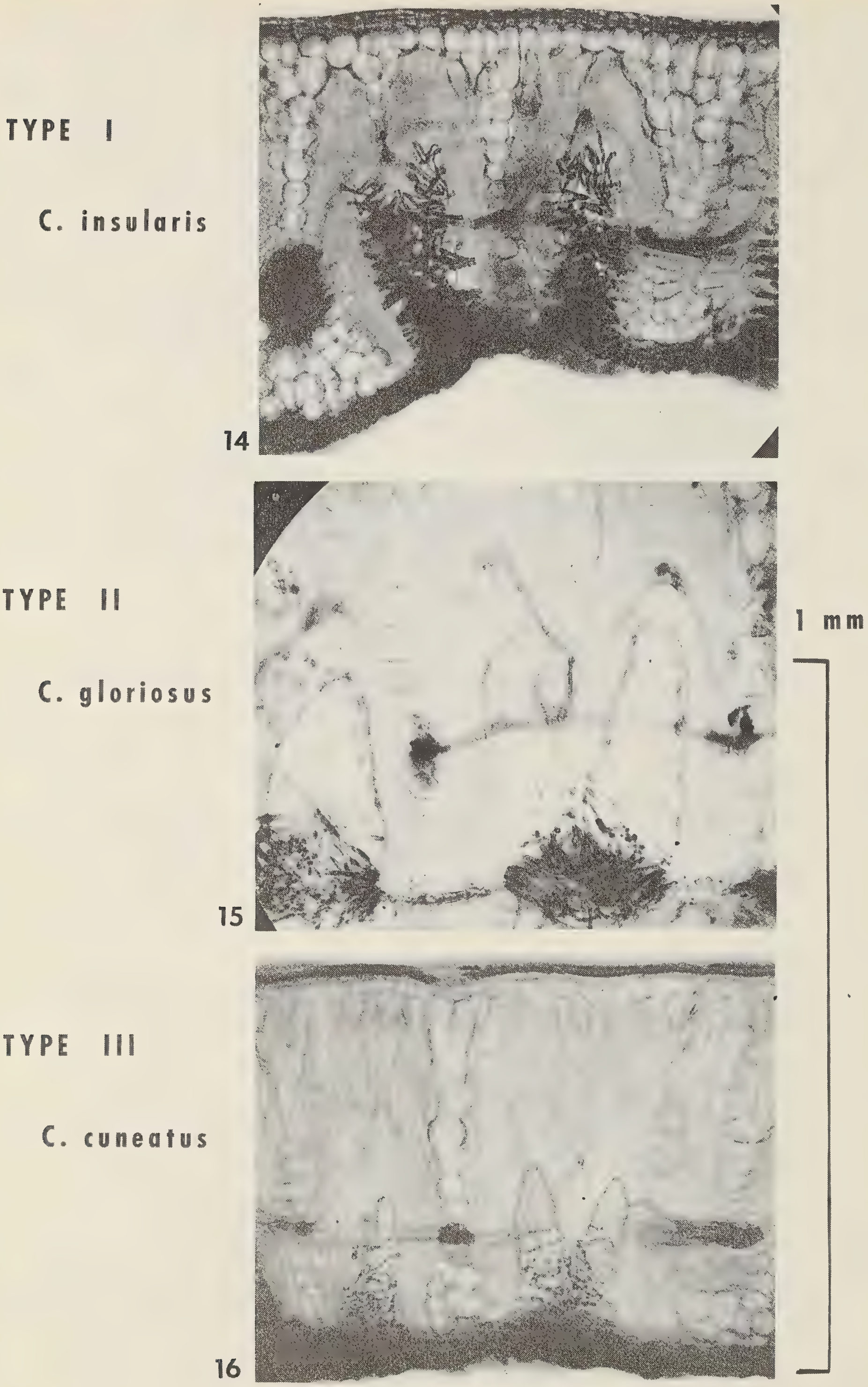
Description as in *C. insularis*.

Mason 563 (UC 634798), Del Monte, Monterey Co.; *Nobs 549-1* & *2*, Sandy Hills, south of Highway 101, 2 miles northeast of junction of Highways 101 and 156, near Santa Rita, Monterey Co.

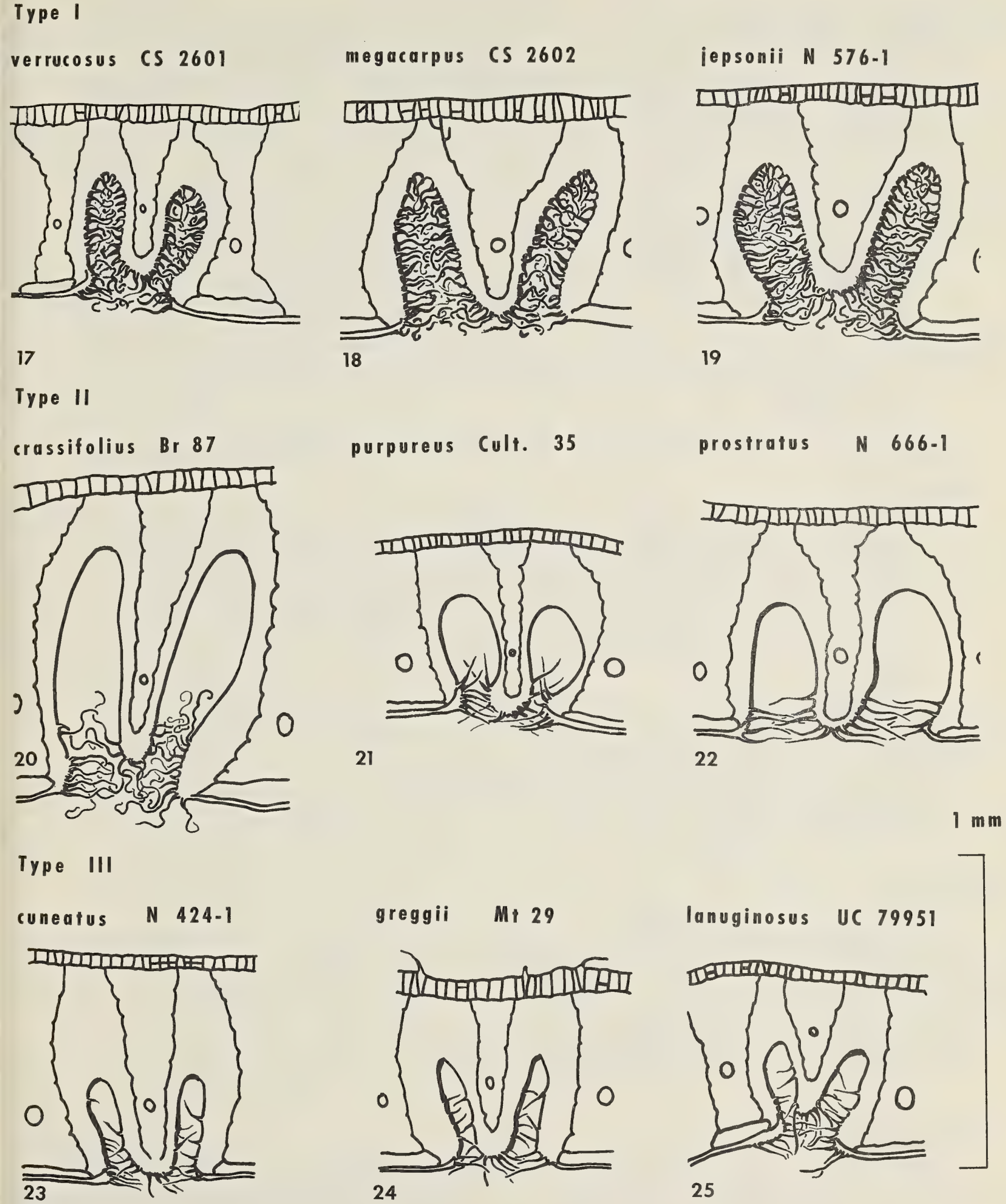
verrucosus Nutt.

Description as in *C. insularis* (fig. 17).

C. F. Smith 2601, Santa Barbara Botanical Garden, Santa Barbara Co.; *McMillan* and *Moran 1519*, Torrey Pines, San Diego Co.



Figs. 14-16. Cleared transections of leaves, showing trichome distribution in the three crypt types of section Cerastes.



Figs. 17-25. Leaf transections, showing trichome distribution and crypt structure in a representative sample of species of section *Cerastes*. Camera lucida drawings.

Type II crypts

gloriosus J. T. Howell

Crypts uniform, narrow at aperture, dilated above; trichomes straight to undulate, interlocking across aperture, and restricted to borders of the aperture and the tips of vein extensions; interior of crypt cavity open (fig. 15).

Nobs *413-1* to *4*, Point Reyes Peninsula, 5 miles inland from lighthouse, Marin Co.; *Nobs* *588-1* to *4*, 1 mile north of Anchor Bay, Mendocino Co.

gloriosus var. *exaltatus* J. T. Howell

Description as in *C*. *gloriosus*.

Nobs *587-1* to *4*, Pine Barrens, 5 miles east of Albion, Mendocino Co.; *Nobs* *679-1* & *2*, 1 mile northwest of Sebastopol, Sonoma Co.

gloriosus var. *porrectus* J. T. Howell

Crypts somewhat variable with a few scattered hairs rising on crypt walls above margins of apertures.

Nobs *410-1* to *4*, Mt. Vision, Point Reyes Peninsula, Marin Co.

crassifolius Torr.

Crypts uniform. As in *C*. *gloriosus*, but trichomes kinky, forming a densely interlocking felt over apertures; interior of crypt naked (fig. 20). These observations do not agree with those of Gemoll (1902, p. 381, fig. 1 from Parry no. 46), where the crypt closely resembles those found in *C*. *greggii* var. *perplexans*, a taxon not recognized by Parry.

K. *Brandegee* *87* (UC 800002), mountains back of Santa Barbara, Santa Barbara Co.; *Acker* *24*, Angeles National Forest, Angeles, Crest Highway between Red Box and Charlston Flat, Los Angeles Co.

crassifolius var. *planus* Abrams.

Description as in *C*. *crassifolius* var. *crassifolius*.

Peterson *160* (UC 569131), Matilija Canyon, Ventura Co.; *Munz* *13162* (UC 569153), Wheeler Hot Springs, Ventura Co.

confusus J. T. Howell

Description as in *C*. *gloriosus*.

Nobs *645-1* to *4*, Rincon Ridge, Sonoma Co.

divergens Parry

Description as in *C*. *gloriosus*.

Nobs *592-1* to *4*, Franz Valley School, Sonoma Co.

pinetorum Cov.

Description as in *C*. *gloriosus*.

Hall and *Babcock* *5272* (UC 64738), Olancha Mountain, Tulare Co.; *Hall* and *Babcock* *5555* (UC 64781), basin of upper Kern River, Tulare Co.; *Bacigalupi*, *Ferris*, and *Wiggins* *2534* (UC 67685), headwaters of Peppermint Creek (tributary of Kern River), Tulare Co.; *C*. *W*. *Sharsmith* *3837* (UC 604529), Funston Creek Drainage on Chagoopa Plateau, Tulare Co.

prostratus Benth.

Crypts quite uniform, characteristically type II in *666*; one plant of *669-3* shows occasional hairs on upper walls of cavity (fig. 22).

Nobs *666-1* to *4*, Forest School, 2 miles northeast of Chico, Butte Co.; *Nobs* *669-1* to *4*, Osborne Hill, 2.5 miles southeast of Grass Valley, Nevada Co.

prostratus var. *laxus* Jepson

Description as in *C*. *gloriosus*.

Nobs *717-1* to *4*, Carnelian Bay, north shore of Lake Tahoe, Placer Co.

prostratus var. *occidentalis* McMinn

Description as in *C*. *gloriosus*.

Nobs *581-1* to *4*, Cobb Mountain, Lake Co.

purpureus Jepson

Description as in *C*. *gloriosus* (fig. 21).

Nobs (culture 35, Univ. Calif. Botan. Garden), from Wooden Valley Grade, Napa Co.

pumilus Greene

Crypts not dilated in upper part, but very narrow with pointed apices; trichomes restricted to apertures and tips of vein extensions, but curving and ascending into crypt cavity.

Nobs *661-1* to *4*, serpentine mountain side 2 miles west of Willow Creek, Humboldt Co.

Type III crypts

cuneatus (Hook.) Nutt.

Crypts uniform; trichomes arising at intervals between stomata, most numerous toward crypt apertures and fewer toward summit (upper one-third nearly glabrous), straight to slightly undulate, loosely associated in crypt cavity. The present observations agree with those of Gemoll (1902) and Cooper (1922) as to general structure of crypt, but both these authors describe the tomentum of the crypt cavity as being dense and feltlike, covering the entire inside walls. This discrepancy is a matter of degree and could be accounted for by the fact that both workers used thin microtome sections which could not show the entire crypt and all its trichomes (figs. 16 and 23).

Nobs *424-1*, Howell Mountain, Napa Co.; *Nobs* *578-1* to *3*, Cobb Mt., Lake Co.; *Nobs* *584-1* & *2*, Orr Springs Road, 2 miles west of Ukiah, Mendocino Co.; *Nobs* *701-1*, Highway 40, 3 miles west of Auburn, Placer Co.; *Wiggins* *8770* (UC 870526), Highway 55, 5 miles north of San Bernardino, San Bernardino Co.; *Wolf* *3865* (UC 729673), Shaver Lake to Big Creek Power House, Fresno Co.; *Hoover* *1985* (UC 766009), 3 miles west of Keystone, Tuolumne Co.

greggii Gray

Description as in *C*. *cuneatus* (fig. 24).

Gillespe (UC 5673), Pinal Mts., Pinal Co., Arizona; *Metcalfe* *29* (UC 130180), Bear Mountain, Silver City, New Mexico.

greggii var. *perplexans* (Trel.) Jepson

Description as in *C*. *cuneatus*.

Wolf *1944* (UC 527233), Hemet Valley, San Jacinto Mts., Riverside Co.; *Hall* *7506* (UC 111537), south fork of upper Santa Ana Canyon, San Bernardino Mts., San Bernardino Co.

greggii var. *vestitus* (Greene) McMinn

Description as in *C*. *cuneatus* (fig. 24).

Hall & *Chandler* *715* (UC 126693), Nelson Ranch, Lee District, Inyo Co.; *Munz* *12780* (UC 494850), San Bernardino Mts., San Bernardino Co.

lanuginosus (Jones) Rose

Description as in *C*. *cuneatus* (fig. 25).

Pringle (UC 79951), Santa Eulalia Mts., Chihuahua, Mexico.

Species with variable crypts

arcuatus McMinn

Crypts variable. In the type collection (*Quick* *2027*), characteristic type II as in *C*. *gloriosus*; in *Bullard* *157*, the hairs are undulate and occur both in apertures and on the lower part of crypt walls, with an occasional hair arising from the walls of the upper part of crypt; in *Constance* *3365*, closely approaching type III as found in *C*. *cuneatus*; in *Constance* *3366* and *3368*, intermediate between type II and type III.

Quick *2027* type (UC 657892), Robb's Peak, Eldorado Co.; *Bullard* *157* (UC 567150), 1 mile southeast of Sage Mill, Madera Co.; *Constance* *3365*, 6.9 miles west of Pinecrest Sonora Road, Tuolumne Co.; *Constance* *3366* and *3368*, 2.7 miles east of Confidence on Sonora Pinecrest Road, Tuolumne Co.

fresnensis Dudley

Crypts variable, ranging from typical type II in *Hall* and *Chandler* *407* to those approaching *C*. *cuneatus* in *Wolf* *3367* and *Constance* *3367*.

Hall and *Chandler* *407* (UC 18332) isotype, Pine Ridge, Fresno Co.; *Wolf* *3684* (UC 729674), road between Shaver Lake and Big Creek Powerhouse, Tuolumne Co.; *Constance* *3367*, 2.7 miles east of Confidence, Sonora-Pinecrest Road, Tuolumne Co.

masonii McMinn

Crypts variable, ranging from type II to type III.

Nobs *419-1* to *5* (Univ. of Calif. Botan. Garden, Berkeley), Bolinas Ridge, Marin Co.; *Nobs* *723-1* to *10*, Bolinas Ridge, Marin Co.

ramulosus (Greene) McMinn

Crypts variable. In *552* and *602* as in *C*. *cuneatus*; in *571*, *572*, *689*, and *723*, the crypts are predominantly like those of *C*. *cuneatus*, but plants included in each of these collections have crypts closely approaching type II (figs. 26 to 34).

Nobs *552-1* to *4*, Tularcitos Ridge, Monterey Co.; *Nobs* *571-1* to *5*, Lagunitas, Marin Co.; *Nobs* *572-1* to *5*, Carson Ridge, Marin Co.; *Nobs* *723-1* to *5*, Mountain Home, Mt. Tamalpais, Marin Co.; *Nobs* *602-1* to *4*, south slopes of Mt. St. Helena, 4.2 miles north of Calistoga, Napa Co.

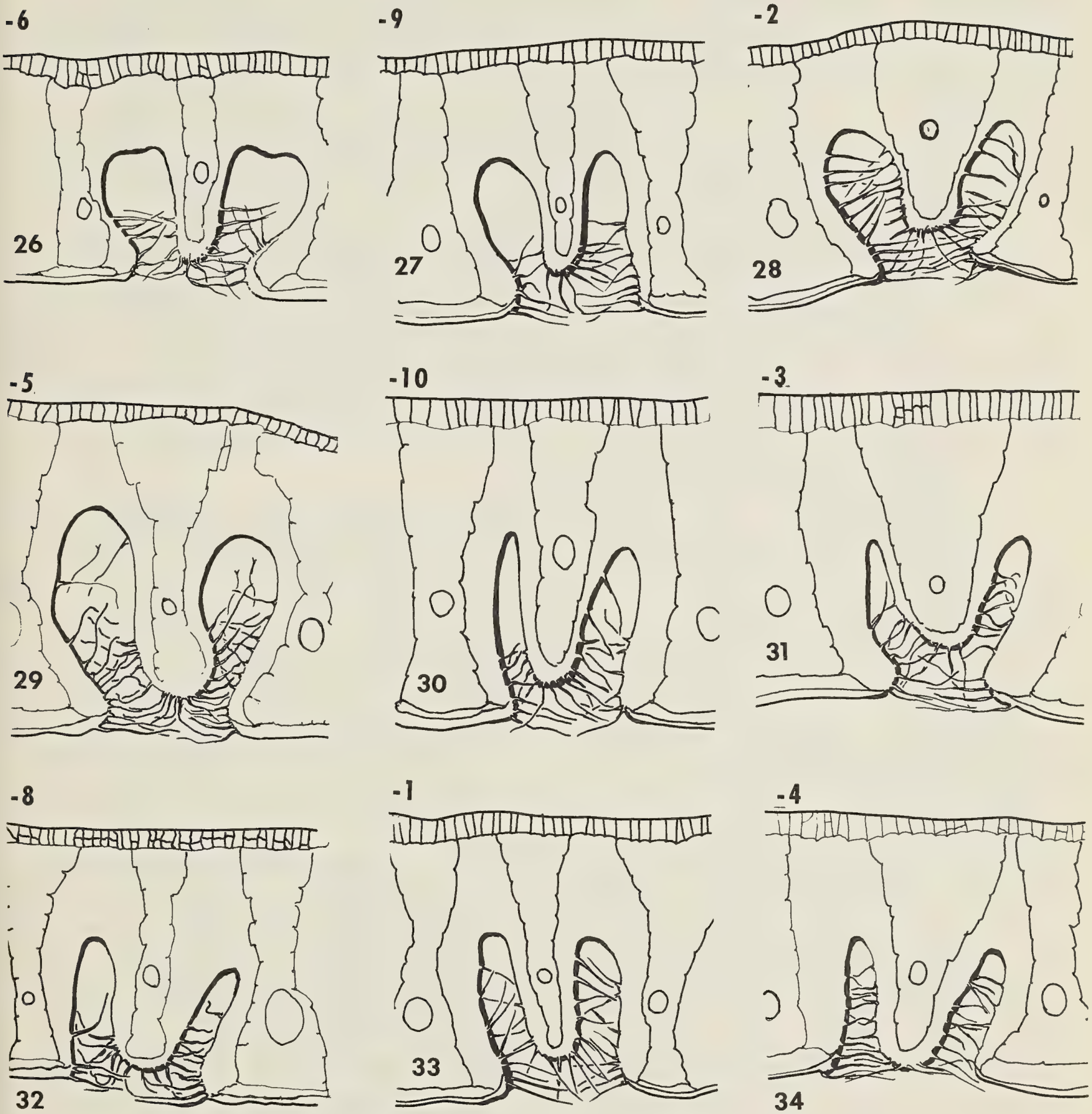
sonomensis J. T. Howell

Somewhat variable, but crypts much as in *C*. *gloriosus* but with trichomes on apertures extending farther up on the crypt walls.

Nobs *422-1* to *9*, Trinity Mt., Sonoma Co.; *Nobs* *685-1* to *4*, Trinity Road 6.5 miles northeast of Glen Ellen, Sonoma Co.

RAMULOSUS

N 687 Hope Valley, Sonoma Co.



Figs. 26-34. Variable crypt structure and trichome distribution among different individuals of one population of Ceanothus ramulosus.

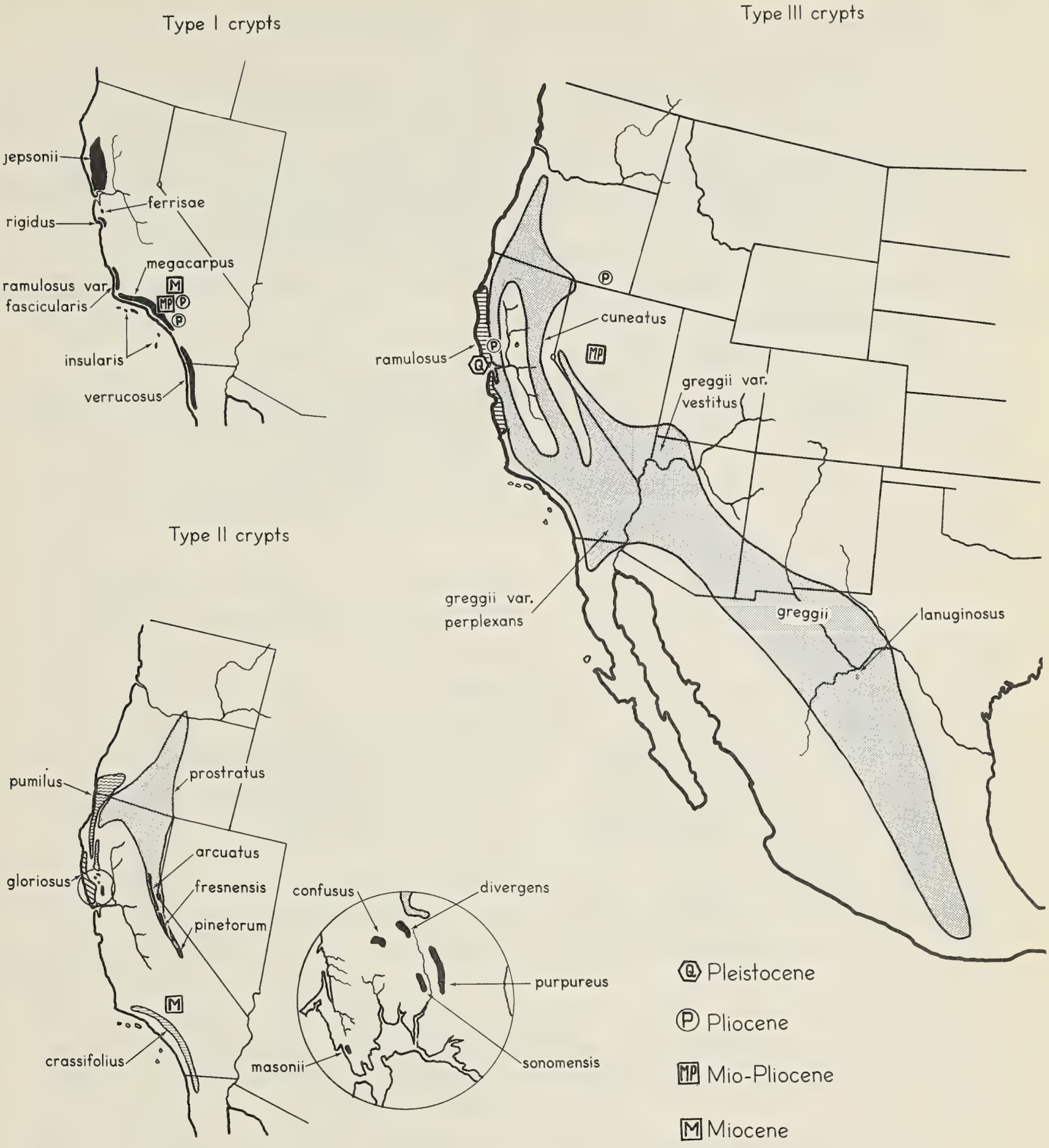
Crypts in hybrids. In controlled garden hybrids, none of the crypt characters exhibit any clear evidence of dominance in the F_1 generation. Species with type I crypts when crossed with species having type II or III produce intermediate-type progeny. When species having the same crypt type are crossed, the F_1 progeny are similar to the parents and show no evidence of recombination effects such as might be anticipated in certain kinds of systems governed by polygenic inheritance.

Natural hybrids that have been studied in the field likewise display intermediate crypt characteristics with respect to the putative parents, as will be shown in more detail in chapter III.

Relation between crypt type and geographical distribution. From study of the distribution of the different species a definite geographical pattern emerges which corresponds to the three different crypt types, as shown in figure 35. The group of species having type I crypts, including *Ceanothus verrucosus*, *C. insularis*, *C. megacarpus*, *C. ramulosus* var. *fascicularis*, *C. ferrisae*, and *C. jepsonii*, are all confined to a narrow strip along the Pacific coast from Baja California north into Humboldt County, California. Each species has a restricted range geographically separated from all the others.

The group having type II crypts, with the exception of *C. crassifolius*, which is found in coastal southern California, is essentially northern. Its distribution pattern forms a large inverted V with its eastern arm extending from the Cascades of central Washington southward to the southern Sierra Nevada of Kern County, California, while its western arm reaches southward only as far as the area immediately north of San Francisco Bay. Included in this group are *C. pinetorum*, *C. prostratus*, *C. pumilus*, *C. gloriosus*, *C. purpureus*, *C. divergens*, and *C. confusus*. *Ceanothus prostratus* has an extensive distribution in the Cascades and Sierra Nevada, the remaining species, as in the former group, having restricted, isolated ranges of distribution.

The *Ceanothus cuneatus-greggii* complex, which includes *C. lanuginosus*, composes the group having type III crypts. Its major distribution is to the southeast, ranging from southern Mexico northward into Texas, New Mexico, Arizona, Utah, and Nevada, with a northwesterly extension occupying nearly all the arid foothills from Baja California north to southern Oregon. This complex, unlike the others, has a nearly semicontinuous distribution throughout its wide range. In its westward extension in California and Oregon it overlaps the ranges of the two other groups. Where members of the *C. cuneatus* complex come into contact with other groups the populations may vary from those containing a few scattered hybrids to others whose members, although highly variable, are so numerous and so strikingly ''intermediate'' between two adjacent taxa that they have been recognized as species. In such populations the crypt types vary from plant to plant and bridge the range from one extreme to the other. Examples are the group with the variable crypts such as *C. ramulosus*, *C. masonii*, *C. sonomensis*, *C. arcuatus*, and *C. fresnensis*, already listed.



Distribution of living and fossil *Ceanothus* section *Cerastes*

Fig. 35. Geographical pattern of the three crypt types and their fossil counterparts. (*Ceanothus arcuatus*, *C. fresnensis*, *C. ramulosus*, and *C. masonii* have variable crypts.)

The western extension of the *C. cuneatus*-*greggii* complex into California, with its many areas of hybridization, appears to represent a more recent spread that has superimposed itself over the older populations composed of taxa having either type I or type II crypts.

The Fossil Record

Rhamnaceous fossils attributed to the genus *Ceanothus* have been reported from various formations in different parts of North America and Europe as early as the Cretaceous. The first specimen, however, that can be identified with a high degree of certainty as a member of this genus is *C. blakei* Chaney. It appears in the Oligocene of the Crooked River basin of central Oregon (Chaney, 1927; Mason, 1942). From this time onward the genus is well represented in the fossil flora, being a more or less constant component of the Madro Tertiary Geoflora of western North America (Axelrod, 1958).

The known fossils of *Ceanothus*, summarized in table 2, show no forms transitional between section *Euceanothus* and section *Cerastes*. It is clearly evident, therefore, that by the late Miocene the genus was already well differentiated with members of both sections represented, and occasionally both are found in the same fossil flora. Also it is apparent that these fossil species occupied much the same general geographical area that living species with similar leaf forms do today (fig. 35).

The section *Cerastes*, the group with which we are primarily concerned, presents its own particular problems. The fossils of this group are limited to detached leaf impressions, which, for the most part, are rather poorly preserved, although the leaf shape, marginal pattern, and gross venation are clearly evident. With the exception of Condit's *C. precuneatus* (U.C. Paleobot. no. 2434) from the Mio-Pliocene Remington Hill flora and Axelrod's *C. precuneatus* (U.C. Paleobot. no. 1737) from the Pliocene Oakdale flora, which do not appear to be members of the genus, all are strikingly similar to leaf forms occurring in living members of section *Cerastes*. Unfortunately the combinations of characters that distinguish living species having similar leaf shapes are, for the most part, lacking in fossils. The result is that all the material is grouped under one name and referred to the most widespread living species with a similar leaf form. In fossil *Cerastes*, 9 of the 11 known specimens are included in *C. precuneatus* Axelrod, and their closest living counterparts are referable to the *C. cuneatus-greggii* complex. The leaf forms of many of these fossils could fit equally well, if not better, into the variation pattern found in *C. megacarpus*, *C. insularis*, or, in some cases, *C. verrucosus*.

The earliest *C. precuneatus* from the Miocene Tehachapi flora (U.C. Mus. Paleobot. no. 1496) is in this category, resembling either *C. megacarpus* or *C. insularis* more closely than it does *C. cuneatus* or *C. greggii*. The same relationship has been suggested for the Mio-Pliocene Mint Canyon material (Mason, 1942). Additional evidence supporting this idea is that in the Tehachapi flora the *Cerastes* fossils are associated with *Lyanothamnus*, and in the Mint Canyon flora with both *Lyanothamnus* and a species in section *Euceanothus* whose closest living counterpart is *C. arboreus* from the channel islands of southern California. The only living member of the section *Cerastes* occurring with these species today is *C. insularis*, a somewhat smaller-fruited insular form of *C. megacarpus*.

TABLE 2. Distribution of Fossil Ceanothi

Flora	Section *Cerastes*	Section *Euceanothus*
	Pleistocene	
Tomales, Marin Co., Calif. (Mason, 1934)	*C. rigidus* Nutt., U.C. Mus. Paleobot. no. 516 (*C. ramulosus* (Greene) McMinn)	*C. thyrsiflorus*, U.C. Mus. Paleobot. no. 517 (*C. thyrsiflorus*)
Napa, Napa Co., Calif. (Axelrod, 1950a)		*C. edenensis* Axelrod, U.C. Mus. Paleobot. no. 3266 (*C. leucodermis* Greene)
Sonoma Co., Calif.	*C. precuneatus* Axelrod, U.C. Mus. Paleobot. nos. 2702, 2702a (*C. cuneatus* (Hook.) Nutt.)	*C.* sp., U.C. Mus. Paleobot. no. 2703
Santa Clara, Santa Clara Co., Calif. (Dorf, 1933)		*C. chaneyi* Dorf, U.C. Mus. Paleobot. nos. 403, 404 (*C. integerrimus* Hook. & Arn.)
	Pliocene	
Mt. Eden, Riverside Co., Calif. (Axelrod, 1937, 1950b)	*C. precuneatus*, U.C. Mus. Paleobot. no. 1002 (*C. insularis* Eastw. or *megacarpus* Nutt.)	*C. prespinosus* Axelrod, U.C. Mus. Paleobot. no. 3330 (*C. spinosus* Nutt.) *C. edenensis*, U.C. Mus. Paleobot. nos. 1000, 1001
Piru Gorge, Los Angeles Co., Calif. (Axelrod, 1950d)		*C. prespinosus*, U.C. Mus. Paleobot. no. 12543
Anaverde, Los Angeles Co., Calif. (Axelrod, 1950c)	*C. precuneatus*, U.C. Mus. Paleobot. nos. 3298, 3299 (*C. verrucosus* Nutt.)	
Muholland, Contra Costa Co., Calif. (Axelrod, 1944a)		*C. prespinosus*, U.C. Mus. Paleobot. no. 1677
Oakdale, Stanislaus Co., Calif. (Axelrod, 1944b)	*C. precuneatus*?,* U.C. Mus. Paleobot. no. 1737	
Alvord Creek, Harvey Co., Oregon (Axelrod, 1944d)	*C. precuneatus*, U.C. Mus. Paleobot. nos. 2134, 2135 (*C. cuneatus*)	

TABLE 2. Distribution of Fossil Ceanothi (concluded)

Flora	Section *Cerastes*	Section *Euceanothus*
	Mio-Pliocene	
Middlegate, Churchill Co., Nevada (Axelrod, 1956)	*C. precuneatus*, U.C. Mus. Paleobot. no. 4404 (*C. cuneatus*-*greggii* complex)	
Clorapagus, Pershing Co., Nevada (Axelrod, 1956)		*C. chaneyi*, U.C. Mus. Paleobot. nos. 4236, 4251
Remington Hill, Nevada Co., Calif. (Condit, 1944)	*C. precuneatus*?† U.C. Mus. Paleobot. no. 2434	
Mint Canyon, Los Angeles Co., Calif. (Axelrod, 1940)	*C. precuneatus* (like *C. insularis* or *megacarpus* Mason, 1942)	*C.* sp. (*C. arboreus*)
	Miocene	
Tehachapi, Kern Co., Calif. (Axelrod, 1939)	*C. precuneatus*, U.C. Mus. Paleobot. no. 1496 (*C. insularis* or *megacarpus* *C. precrassifolius* Axelrod, U.C. Mus. Paleobot. nos. 1494, 1495	
	Oligocene	
Gray Ranch, Crooked River Basin, Crook Co., Oregon (Chaney, 1927)		*C. blakei* Chaney, U.C. Mus. Paleobot. nos. 95, 98 (*C. sanguineus* or *velutinus*)

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*This fossil is a leaf fragment showing a serrate margin unlike any known *Ceanothus*.

†This is a very poorly preserved specimen; although it has the gross shape of a leaf of *C. cuneatus* the impression appears to have been made by a thin leaf. The venation pattern and the finely serrate leaf margin do not resemble any known *Ceanothus*.

The specimen of *C. precuneatus* from the Pliocene Mt. Eden flora (U.C. Mus. Paleobot. no. 1002) likewise resembles *C. megacarpus* more closely than it does either *C. cuneatus* or *C. greggii*, and, as Axelrod (1950b) indicated, it is associated with species characteristic of coastal chaparral rather than with interior forms. The fossils from the Pliocene Anaverde flora (U.C. Mus. Paleobot. nos. 3298 and 3299) bear a strong resemblance to *C. verricosus* and might have a closer relationship to this species than to *cuneatus* or *megacarpus*, as suggested by Axelrod (1950b). From the material at hand, these southern California fossils appear to represent early elements of the present coastal species with type I crypts.

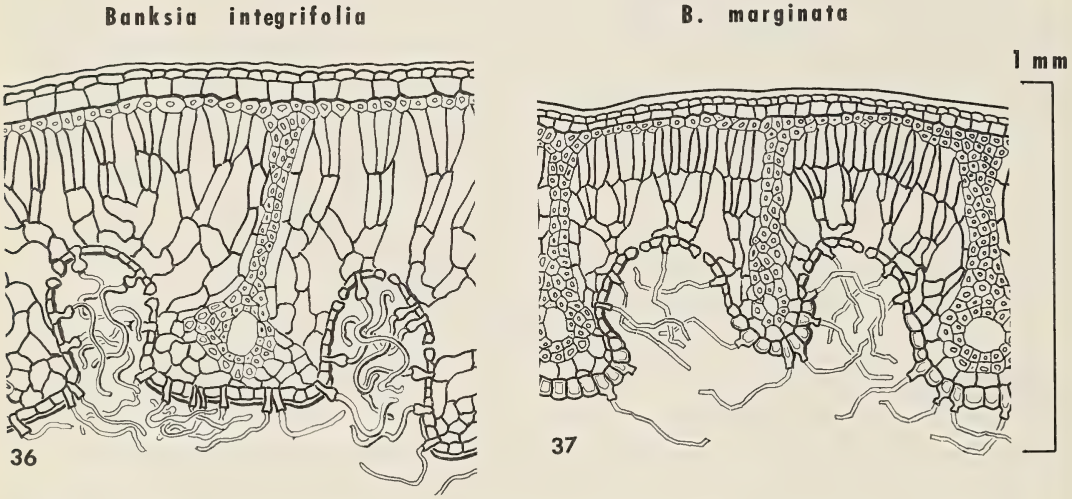
Fossils from the Great Basin area Mio-Pliocene Middlegate flora (U.C. Mus. Paleobot. no. 4404) and the early Pliocene Alvord Creek flora (U.C. Mus. Paleobot. nos. 2134 and 2135) are close counterparts of leaves found on living members of the *C. cuneatus-greggii* complex; at that time, as today, these forms occupied a continental situation. Late Pliocene fossils from the Sonoma flora (U.C. Mus. Paleobot. nos. 2702 and 2702a) likewise appear to be members of this complex, for they are nearly exact replicas of *C. cuneatus*. These fossils are of great interest because they indicate that by this geological era at latest the predominately interior element had spread into California.

Another element of the section *Cerastes* had also arisen at the time of the Miocene. In the Tehachapi flora, two leaf impressions designated as *C. precrassifolius* Axelrod (U.C. Mus. Paleobot. nos. 1494 and 1495) are present. Number 1494 in particular bears a strong resemblance to its living counterpart. As in the living species, the leaf has coarsely spinulose teeth and is of heavy texture, with prominent tertiary veinlets and raised areas between the casts of the crypts. These fossils provide evidence that at least one member of the group of *Cerastes* having the open type II crypts had differentiated at this early date.

One remaining fossil of *Cerastes* has been found in the Pleistocene Tomales Bay flora (U.C. Mus. Paleobot. no. 517) and designated *C. rigidus* Nutt. (Mason, 1934). Present observations bear out Mason's later (1942) conclusions that it is more closely related to *C. ramulosus*, a species to be discussed in detail later.

The origin of section *Cerastes* with its unusual leaf modifications still remains obscure. No forms, either living or fossil, have been found that show transitions between the leaf types of the two sections *Euceanothus* and *Cerastes*. The hypothesis that *Cerastes* evolved under maritime conditions (Mason, 1942), with later migration and establishment in interior situations, deserves consideration. Mason cites several genera which he believes to have had such a history. Another point stressed by the same writer is that all the species of *Ceanothus* in section *Cerastes* that have alternate leaves, a characteristic primarily of members of section *Euceanothus*, as in *C. insularis*, *C. megacarpus*, and *C. verrucosus*, are maritime. Additional evidence in support of the hypothesis of maritime origin is that, in several different families, species having leaves with crypts structurally similar to those of *Cerastes* are found along the coast in other parts of the world.

In the Proteaceae, for example, the type of crypt described by Hamilton (1907) in *Banksia serrata* L., a coastal species of southeastern Australia and Tasmania (Ewart, 1930), is very similar to that found in the *Cerastes*. Two additional species, *Banksia integrifolia* L. (coast *Banksia*) and *B. marginata* L., found in the coastal regions of southeastern Australia, also have similar crypts (Figs. 36 and 37). *Dryandra floribunda* R. Br., occurring from King Georges Sound to the Swan River in Western Australia, has the same structural adaptation (Shelton, 1921), and so have two species of fig (Moraceae), *Ficus macrophylla* Desf. and *F. rubiginosa* of coastal eastern Australia (Hamilton, 1907).



Figs. 36-37. Leaf transections of two species of *Banksia*, showing similarity of anatomical structure to *Ceanothus*, section *Cerastes* (cf. fig. 13). *Banksia integrifolia*, U.C. herbarium 46298, Port Jackson, New South Wales, Australia, and *B. marginata*, Davis 1102, Table Mountain, Tasmania, Australia.

However, the selective advantage of a cryptose leaf over one with stomata flush on the lower surface in a maritime environment has not been demonstrated. Such a structure might conceivably have been selected by other environmental factors, such as a prolonged seasonal dry phase, or even by fortuitous establishment. *Nerium oleander* L., which extends from Portugal into the Middle East, is not essentially maritime, but it has similar crypts (Metcalfe and Chalk, 1950) and, like all the above-mentioned examples, occurs in a climate having an extended arid period. Certain species of the tropical American genus *Mouriri* (Melastomaceae) also have stomatal crypts (Morley, 1953). According to Morley's interpretation, these structures have arisen independently in at least two evolutionary lines in this genus, and he was unable to find any environmental preference which would suggest that crypts provide a selective advantage.

The available evidence does indicate, however, that the cryptose leaf in section *Cerastes* is derived from the less-specialized leaf found in section *Euceanothus*. This differentiation must have arisen before the Miocene era, for by late Miocene the section had already achieved a wide geographical distribution. The leaf forms of these fossils suggest also that considerable differentiation had occurred within the section, because forms related to all three different crypt types were present.

CHAPTER II

CYTOGENETIC STUDIES

A genus of woody plants such as *Ceanothus*, which requires from three to five years to mature a single generation, is scarcely suitable material for detailed genetic study. Nevertheless, to clarify the taxonomic status of the numerous forms intermediate between species found in the field, and to obtain specific experimental data needed for interpreting the genetics of the variation pattern in the genus, a limited number of hybrids were made. They were planned with three objectives in mind: (1) to determine the degree of genetic compatibility between members of the two sections *Euceanothus* and *Cerastes*, (2) to determine the compatibility between members of taxa within the section *Cerastes*, and (3) to explore the genetic composition of plants intermediate between recognized species that are of frequent occurrence in the wild.

Methods. Hybrids between the sections and within the section *Cerastes* were made, for the most part, upon cultivated plants of known origin growing in Berkeley in the garden of Professor H. L. Mason or in the Arboretum of Tilden Regional Park, Oakland. The genetic base was broadened by using pollen collected from plants of natural populations in the field and also by making controlled interspecific hybrids between individuals in natural populations.

Preliminary studies demonstrated that emasculation had too severe an effect upon further floral development to make it a practical procedure in producing hybrids within the genus. In 20 trials, 10 each on *C. gloriosus* and *C. masonii*, the entire inflorescence aborted before artificial pollination was possible.

This necessitated an alternative technique. Inflorescences on all the parental plants were covered with parchment bags before anthesis. At anthesis the bags were carefully removed, and the pollen collected from the staminate parent was applied directly to the stigmas of the maternal parent; the inflorescence was then carefully rebagged. The protective bag was left on the inflorescence until the stigmas were no longer receptive, a period of five to seven days. At this time the bag was removed and the fruit was left to develop without further protection. To prevent seed loss when the fruit dehisced, light bags made of nylon were placed over the entire fruiting inflorescence. With each interspecific cross made in this way, a selfing was attempted simultaneously whenever possible.

This method was a success, because parent plants used as females in crosses involving *C. rigidus*, *C. prostratus* var. *occidentalis*, *C. jepsonii*, *C.*

gloriosus and its var. porrectus proved to be self-incompatible. When the maternal parent was partially self-fertile, the progeny from selfing were grown in addition to the interspecific hybrids. The seedlings of the hybrids could readily be distinguished from those of the parent species by their intermediate appearance. Comparison of the progeny of reciprocal crosses further substantiated their hybrid origin.

The technique followed for the study of the genetic constitution of intermediate forms found in the field was essentially the same as that described above. Plants that appeared to be F_1's were used as parental material in the crosses. By selfing or intercrossing these supposed F_1's, the recombination and segregation of characters in the resulting progeny could be studied.

Intersectional hybrids. During the present study, 33 attempts were made to obtain 11 different combinations between members of the section Euceanothus and those of section Cerastes. In each trial no fewer than 250 individual flowers were artificially pollinated. Figure 38 summarizes the results.

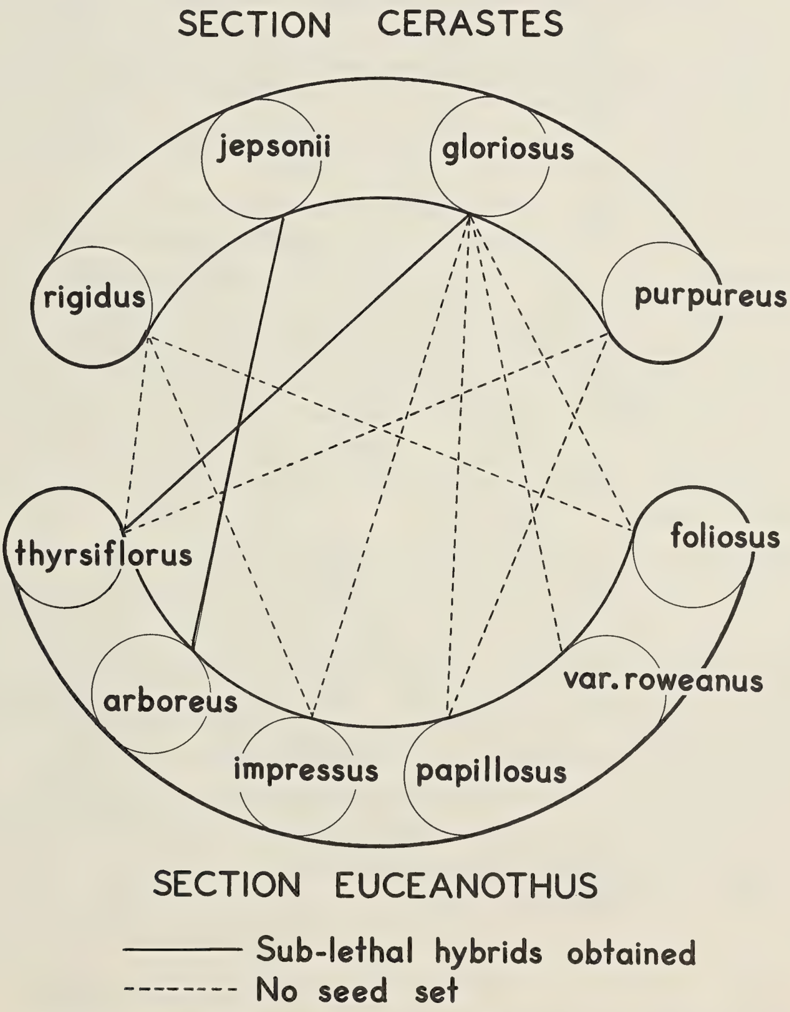


Fig. 38. Summary of results from crosses between members of the sections Euceanothus and Cerastes.

Only two of these attempts were partly successful; *gloriosus* × *thyrsiflorus* yielded seven well filled seeds, two of which, on germination, proved to be induced selfs of *C. gloriosus*, but the remaining five were hybrids, all uniformly weak and surviving no longer than 10 months. The most vigorous plant produced six branches which did not exceed 18 cm in length. The other partly successful cross, *C. arboreus* × *C. jepsonii*, yielded twenty good seeds from which four seedlings were obtained. One of these proved to be an induced self of *C. arboreus*; the other three were weak hybrids. Although the hybrids lived for more than a year, they never developed normally; the most vigorous at the time of its death had produced only a single stem, 14 cm long.

The difficulty in obtaining intersectional hybrids is clearly indicative of a deep-seated genetic barrier between the sections *Euceanothus* and the *Cerastes*. In garden cultures only two have been reported (McMinn, 1942), and in nature only six are known to the author, although species from the two sections commonly flower side by side. Strong internal barriers apparently have evolved between the sections which not only act to inhibit fertilization but, when it does occur, yield progeny that are so weak that they rarely reach maturity.

Interspecific hybrids within section Cerastes. In contrast with the incompatibility found between the sections, species within section *Cerastes* are interfertile. Twenty of the twenty-four interspecific hybrid combinations attempted have been successfully obtained, as shown in table 3. The results of these studies are summarized in figure 39. All four of the unsuccessful hybridizations were attempted in natural populations in the field and appear to be accidental failures, for in each case fruit was set but the seed was lost before harvest.

Seven of the interspecific combinations have been carried to the second generation. Small F_2 populations of *C. gloriosus* × *C. masonii*, *C. gloriosus* × *C. rigidus*, and *C. gloriosus* var. *porrectus* × *C. rigidus* were grown by Dr. Lee W. Lenz at the Rancho Santa Ana Botanic Garden at Claremont, California; the combinations *C. gloriosus* × *C. cuneatus*, *C. gloriosus* × *C. masonii*, and *C. rigidus* × *C. jepsonii* are being studied by the author in the gardens of Carnegie Institution of Washington at Stanford, California.

Although the limited number of individuals in each population precludes any kind of Mendelian genetic analysis, the following observations are of interest. In all the F_1 hybrids no character was found that exhibited simple dominance, the F_1 populations being intermediate between the parental species in all respects. Individual members in each F_1 population, however, varied from plant to plant in the expression of specific characters, giving a narrowly segregating array that revealed considerable heterozygosity in the genotypes of the parents. The F_1 hybrids, without exception, were characteristically vigorous and had a much higher survival rate than the parental species when grown under similar garden conditions at the University of California Botanical Garden or at the gardens of Carnegie Institution at Stanford.

TABLE 3. Hybridizations within the Section *Cerastes*

Species	Number of			Culture Number
	Flowers	Fruit	Seed	
608-1 *C. confusus*, Rincon Ridge, Sonoma Co., F[*]				
× Self, F	120	0	0	...
× 608-2, F	98	18	0[†]	...
× 425-1 *C. purpureus*, Howell Mt., Napa Co., F	88	16	0[†]	...
× 615 *C. gloriosus*, Anchor Bay, Mendocino Co., T.P.A.	82	12	0[†]	...
B *C. gloriosus*, Pt. Reyes, Marin Co., H.L.M.				
× Self, H.L.M.	120	0	0	...
× 615 *C. gloriosus*, Anchor Bay, Mendocino Co., H.L.M.	80	20	50	...
× C *C. cuneatus*, NE Napa Co., H.L.M.	93	27	68	X4
× A *C. masonii*, Bolinas Ridge, Marin Co., H.L.M.	98	25	54	X3
615 *C. gloriosus*, Anchor Bay, Mendocino Co., T.P.A.				
× Self, T.P.A.	100	0	0	...
× B *C. gloriosus*, Pt. Reyes, H.L.M.	85	26	64	...
× 915-1 *C. crassifolius*, Angeles National Forest, Los Angeles Co., T.P.A.	100	30	85	X260
× 631-1 *C. gloriosus* var. *porrectus*, Mt. Vision, Marin Co., T.P.A.	150	38	78	X28
× 512 *C. cuneatus*, Mt. Diablo, Contra Costa Co., F	30	4	9	X53
× 612 *C. rigidus*, Huckleberry Hill, Monterey Co., T.P.A.	94	14	34	X69
576 *C. jepsonii*, Mt. Tamalpais, Marin Co., F				
× B *C. gloriosus*, Pt. Reyes, Marin Co., H.L.M.	18	2	4	X97
409-1 *C. jepsonii* var. *albiflorus*, Knoxville, Napa Co., F				
× 426-1 *C. cuneatus*, Monticello, Napa Co., F	30	4	12	X17
× 615 *C. gloriosus*, Anchor Bay, Mendocino Co., T.P.A.	23	3	5	...
× 408-23 *C. purpureus*, Wooden Valley Grade, Napa Co., F	16	3	5	X18
A *C. masonii*, Bolinas Ridge, Marin Co., H.L.M.				
× Self, H.L.M.	90	13	31	X7
× C *C. cuneatus*, Napa Co., H.L.M.	160	22	46	X9
× C *C. gloriosus*, Pt. Reyes, Marin Co., H.L.M.	96	14	38	X10
× 409-1 *C. jepsonii*, Knoxville, Napa Co., F	165	29	68	X11

TABLE 3. Hybridizations within the Section *Cerastes* (concluded)

Species	Number of			Culture Number
	Flowers	Fruit	Seed	
614 *C. prostratus* var. *occidentalis*, Cobb Mt., Lake Co., T.P.A.				
× 624-1 *C. purpureus*, Atlas, Napa Co., F	134	27	50	X83
408-36 *C. purpureus*, Wooden Valley Grade, Napa Co., T.P.A.				
× 512 *C. cuneatus*, Mt. Diablo, Contra Costa Co., F	23	3	7	X54
× 615 *C. gloriosus*, Anchor Bay, Mendocino Co., T.P.A.	60	9	23	X36
× 612 *C. rigidus*, Huckleberry Hill, Monterey Co., T.P.A.	30	5	13	X39
612 *C. rigidus*, Huckleberry Hill, Monterey Co., T.P.A.				
× Self, T.P.A.	90	0	0	...
× 611 *C. rigidus*, Huckleberry Hill, Monterey Co., T.P.A.	60	9	25	X96
× 512 *C. cuneatus*, Mt. Diablo, Contra Costa Co., F	140	26	60	X52
× 615 *C. gloriosus*, Anchor Bay, Mendocino Co., T.P.A.	50	7	19	X63
× 613 *C. gloriosus* var. *porrectus*, Mt. Vision, Marin Co., T.P.A.	175	50	98	X67
× 576 *C. jepsonii*, Mt. Tamalpais, Marin Co., F	98	20	64	X66
× A *C. masonii*, Bolinas Ridge, Marin Co., H.L.M.	70	12	32	X62
500-1 *C. ramulosus*, Mt. Tamalpais, Marin Co., F				
× 576 *C. jepsonii*, Mt. Tamalpais, Marin Co., F	120	32	0[†]	...
× 512 *C. cuneatus*, Mt. Diablo, Contra Costa Co., F	85	16	0[†]	...

[*] F = field hybridization; T.P.A. = hybridization performed in the Tilden Regional Park Arboretum; H.L.M. = hybridization performed in the garden of Professor H. L. Mason.

[†] Fruit set but lost before harvest.

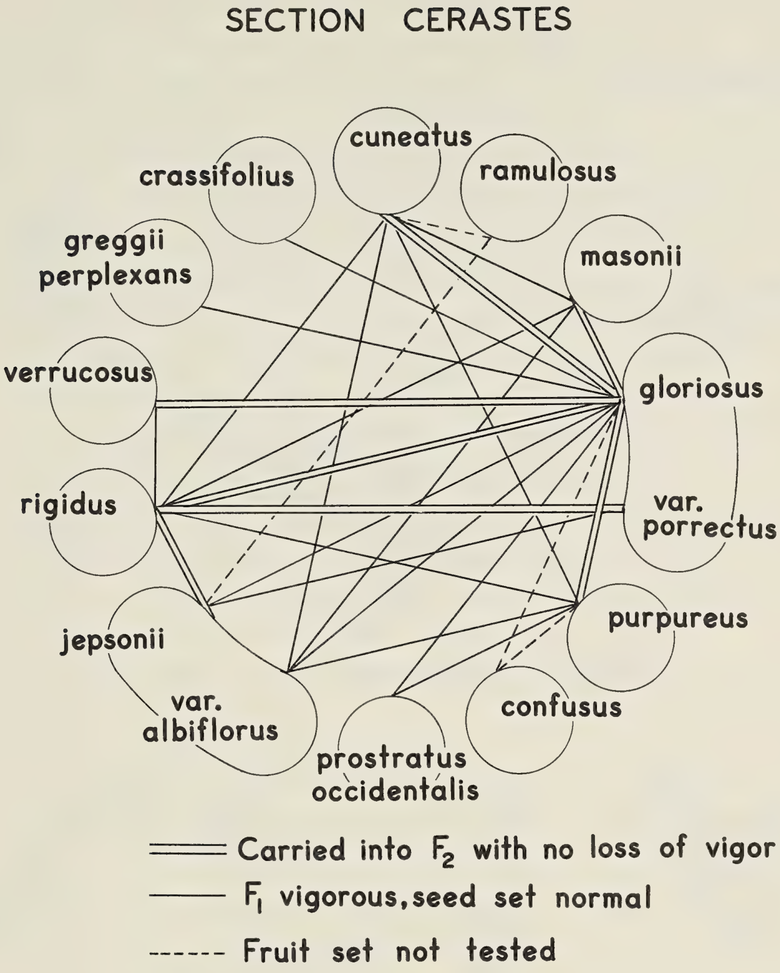


Fig. 39. Summary of results from crossing species within section *Cerastes*.

All the interspecific hybrids between members of the *Cerastes* section had normal seed set and high pollen fertility, as indicated in tables 3 and 9. The second-generation progeny showed no evidence of weakness that would indicate latent genetic incompatibility between the parental forms.

The cross between *C. gloriosus*, a prostrate blue-flowered species from the coastal bluffs of Point Reyes, and the strictly erect white-flowered *C. cuneatus* from the interior typifies the pattern found in these crosses. All five F_1 plants grown at the University of California Botanical Garden were decumbent but varied strikingly in the intricacy of their branching pattern. Figure 40 shows habit sketches of 1-year-old seedlings of the parental species and the F_1, and a

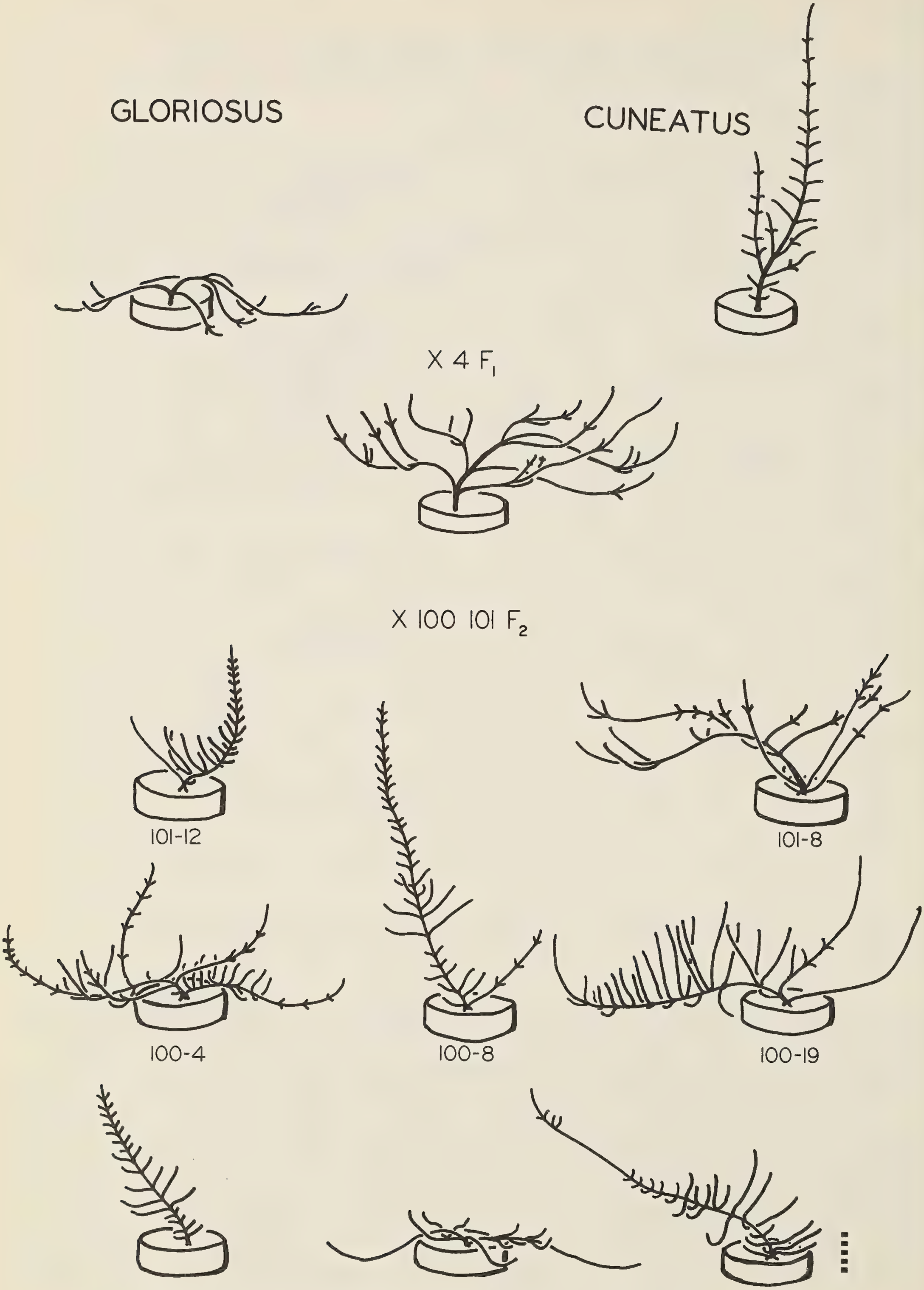


Fig. 40. Segregation in habit characters among F_2 progeny of the cross *Ceanothus gloriosus* × *C. cuneatus*.

selected group of F_2 seedlings of similar age. In the early seedling stages of this small population of thirty-four F_2 plants, the inheritance of prostrate habit as contrasted with erect appeared to be simple: eight plants had completely prostrate central leaders, nineteen were semierect, and seven had strictly erect central leaders. At this stage the population seemed to fit a 1:2:1 ratio, suggesting the action of a single gene pair controlling this character. As the plants developed, however, this apparently simple situation vanished, no two plants being alike. Although there was a wide array of variants, both truly prostrate and strictly erect forms characteristic of the parents were lacking.

The inheritance of flower color in this cross also appears to be complex. Flowers of the parental plant of *C. gloriosus* used in this cross were deep blue, and those of *C. cuneatus* creamy white. None of the five F_1 plants were of the same shade, although all were intermediate, being very pale blue. Among the F_2 population, consisting of thirty-four plants, no two individuals could be matched in color, which ranged from bluish-white through shades of pale blue, blue, and blue-lavender to a deep blue-violet. In one individual the deep blue-violet exceeded in intensity the color of the *C. gloriosus* parent. The creamy white color of the *C. cuneatus* parent, however, has not been recovered. F_2 plants also showed variation in stability of color: some had flowers that bleached on aging, whereas in others the color became more intense.

The five contrasting vegetative characters listed below have been analyzed in this population.

Character	*C. gloriosus*	*C. cuneatus*
Leaves	Angle between veins and midrib greater than 40°	Angle between veins and midrib under 20°
Leaves	Margins spinulose-dentate, with more than 18 dentations per leaf	Margins entire
Stipules	Reflexed at maturity	Erect at maturity
Year-old twigs	Strongly ridged between the nodes	Smooth and entire
Year-old twigs	Bark color maroon-red	Bark color silvery gray

Although the number of individuals in this population is small, it is evident that there is relatively free recombination between these characters among the F_2 progeny, as is shown in table 4. This is of particular interest because similar recombination patterns occur in many natural populations, as will be discussed in chapter III.

Genotypic composition of field intermediates. The first critical field studies on the genus by Parry (1889a and b) and Brandegee (1894) called attention to the

TABLE 4. Recombination Frequencies of Five Contrasting Characters among the F_2 Progeny of C. gloriosus × cuneatus

Stipules	Number of Dentations per Leaf	Branchlets	Color of Mature Bark								
			Gray			Intermediate			Red		
			Angle of Secondary Vein and Midrib								
			20° to 30°	31° to 40°	41° to 50°	20° to 30°	31° to 40°	41° to 50°	20° to 30°	31° to 40°	41° to 50°
Ascending	0- 6	S*									
		I									
		R									
	7-12	S									
		I				1					
		R					1				
	13-18	S		1							
		I				2					
		R				3				1	
	18-24	S									
		I					1				
		R					1				
Intermediate	0- 6	S									
		I									
		R									
	7-12	S									
		I						1			
		R				1		2			
	13-18	S	1								
		I									
		R				4	1	1			
	18-24	S									
		I									
		R					2				
Reflexed	0- 6	S					1				
		I									
		R									
	7-12	S				1					
		I					1	1		1	
		R					1				
	13-18	S									
		I									
		R				1	2				
	18-24	S									
		I									
		R							1		

*S = smooth; I = intermediate; R = ridged.

prevalence of natural hybrids between the species of *Ceanothus*. Since that time this aspect of the biology of the genus has received considerable attention, at least forty-two different hybrid combinations having now been reported. The majority of these hybrids are well substantiated by their immediate morphology. None of these had been confirmed by genetic tests, and no data were available on the vigor or viability of later generations. The present work has amply confirmed the hybrid origin of these entities through the synthesis of controlled hybrids. In addition, three progeny tests of field intermediates made during this study deserve special attention. The first two, which involve *C. jepsonii*, the serpentine endemic, provided data unobtainable from controlled hybrids, for this species, as well as its hybrids, requires from 6 to 10 years to mature a single generation.

Although these garden-grown progenies consisted of very small numbers, they have yielded significant information. The progeny from selfed or mutually pollinated plants that were intermediate between *C. jepsonii* and *C. cuneatus*, and between *C. jepsonii* and *C. ramulosus*, show recombination types approaching the characters of the probable parents. This can be clearly seen in leaf characters. Figure 41 illustrates the variation in leaves of the parental species, the two field intermediates used for mutual pollination at Bootjack Camp, and twelve of the resulting progeny grown in the Botanical Garden of the University of California at Berkeley. Although the exact parental types have not been recovered among the segregating progeny, plants X98-9 and 99-4 closely resemble *C. jepsonii*, whereas plant 98-1 approaches *C. ramulosus*.

In these progeny not all the characters segregate as widely as the leaf characters. For example, the number of floral segments in all plants was found to be intermediate between those of the parental species, and, like the artificial F_1 hybrids, there were approximately equal numbers of both pentamerous and hexamerous flowers.

With the exception of one weak dwarf, all the progeny from the field hybrid *jepsonii* × *ramulosus* were vigorous, produced flowers, and set good fruit. This contrasted sharply with the ten plants of *C. jepsonii* grown simultaneously from open pollinated seed obtained from the Bootjack Camp population. In the same garden these plants were weak and stunted, none surviving to maturity. A similar situation was found among the eight progeny resulting from self-polinating a plant intermediate between *C. jepsonii* var. *albiflorus* and *C. cuneatus* as compared with ten weak plants of typical *C. jepsonii* from Knoxville in Napa County.

A quite different situation was found among progeny of the intermediate between *C. prostratus* and *C. cuneatus*. Of twenty-five seeds that were obtained only twelve germinated; they were weak and slow growing, and they developed their first regular leaves ten to twelve days later than seedlings of *C. cuneatus* and *C. prostratus* var. *occidentalis* that were germinated at the same time. After three months all but two of the original twelve seedlings had died, and three years later each of the two survivors had produced only a single shoot

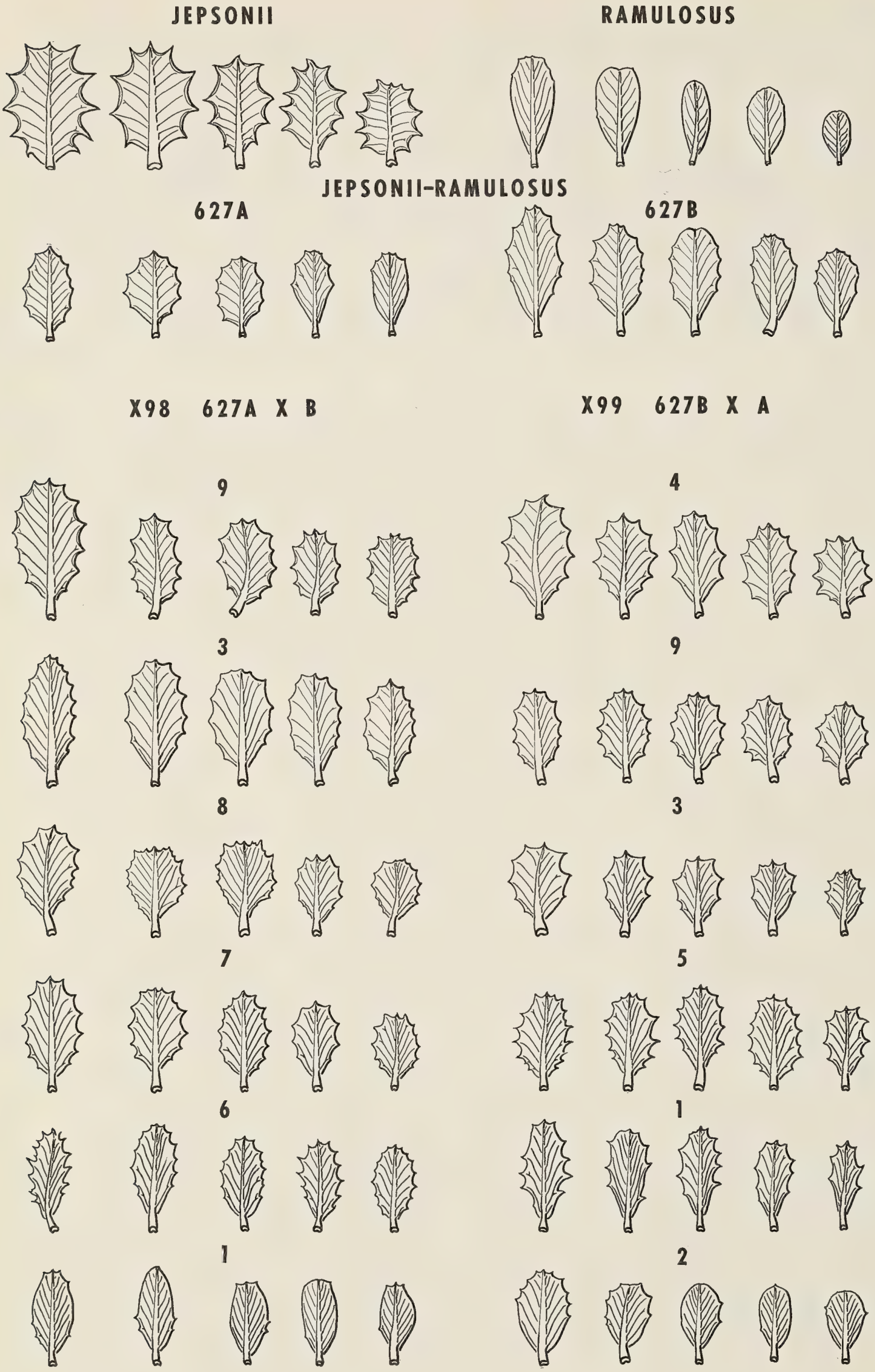


Fig. 41. Segregation in leaf characters among progeny of field intermediates between Ceanothus jepsonii and C. ramulosus. See text.

approximately 12 cm long. In contrast, seedlings of pure *C. prostratus* var. *occidentalis* of the same age growing in the same garden at Berkeley were vigorous and highly branched, the smallest plant among them covering an area 45 by 62 cm.

This evidence suggests that there may be some genetic incompatibility between *C. prostratus* and *C. cuneatus*, yet these taxa are known to hybridize commonly in the wild. In the foothills of the Sierra Nevada from Fresno County north into Modoc County, *C. prostratus* is frequently found adjacent to *C. cuneatus*. In all these areas plants intermediate between the two species are found. They vary in frequency from a few scattered plants in the zones of immediate contact in undisturbed areas to extensive hybrid swarms where the natural habitat has been altered by agriculture and grazing.

An example is the population of X*C. connivens* (Greene) McMinn in an abandoned orchard in Nevada County, analyzed by the present author and reported by McMinn (1944, histogram 3, pls. 35 and 36). In this variable population, which is intermediate between *C. prostratus* and *C. cuneatus*, a sample of ten variable and obviously segregating intermediate plants showed no irregularities in meiosis in pollen mother cells and had normal pollen and seed. The common occurrence of such populations over this broad area indicates that here, as in the remainder of the species in section *Cerastes*, no significant genetic barriers to intercrossing exist.

Cytology. In all species of *Ceanothus* studied, the somatic chromosome complement consists of 12 chromosome pairs. The first observation in the genus was made by Bowden (1940), who reported a haploid number of 12 in *C. americanus* from Clarke County, Virginia. McMinn, in his monograph of the genus (1942), lists counts made by the present author for fifteen species and two varieties in section *Euceanothus* and seven species and two varieties in section *Cerastes*. All these had $2n = 24$ chromosomes.

Ten additional species and three varieties have been studied in section *Cerastes*, and two additional species and one variety in section *Euceanothus*, as listed in table 5 and illustrated in figures 42 to 65. The same somatic number of 24 chromosomes was found in all the entities, bringing the number of species on which chromosome counts have been made to thirty-four out of the total of fifty-five recognized by McMinn.

There is striking uniformity in the karyotypes of the genus. The chromosomes are small, ranging in length from about 2 microns in the smallest to about 5 microns in the largest. In the species studied there are four relatively large chromosome pairs with median centromeres which range in length from about 4 to 5 microns, and eight small pairs about 2 to 3 microns long which have subterminal centromeres, as shown in figures 42 and 46. No satellites or secondary constrictions have been observed.

The division of the microspore mother cells into microspores is regular and of the simultaneous type, as described by Maheshwari (1950). There is a

TABLE 5. Chromosome Number and Cytological Behavior in Natural Taxa in Ceanothus

Species	Source	Chromosome Number	Chiasma Frequency	Percentage Normal Pollen	Grains Counted
		Euceanothus			
C. thyrsiflorus var. repens					
fig. 42	256 commercial	24	. . .	. . .	. . .
C. parvifolius	Tuolumne Grove, Tuolumne Co.				
fig. 43	924	24	. . .	. . .	. . .
C. impressus	Surf, Santa Barbara Co.				
fig. 44	919	12_{II}	. . .	. . .	. . .
C. papillosus var. roweanus	Mt. Tranquillon, Santa Barbara Co.				
fig. 45	923	12_{II}	. . .	. . .	. . .
		Cerastes			
C. confusus	Rincon Ridge, Sonoma Co.				
fig. 47	608-1	12_{II}	1.35	87	658
	608-3	12_{II}	. . .	. . .	. . .
C. crassifolius	Angeles National Forest, Los Angeles Co.				
fig. 48	915	12_{II}	. . .	. . .	. . .
C. divergens	Franz Valley School, Sonoma Co.				
fig. 49	477-1	12_{II}	1.37	95	548
	477-2	12_{II}	. . .	. . .	. . .
C. gloriosus	Point Reyes, Marin Co.				
figs. 46, 50	B	12_{II}	1.37	96	542
	Anchor Bay, Mendocino Co.				
fig. 51	615	12_{II}	. . .	94	534
C. gloriosus var. exaltatus	7 mi E of Albion, Mendocino Co.				
fig. 52	578-1	12_{II}	. . .	95	687
	578-4	12_{II}	. . .	72	663
C. gloriosus var. porrectus	Mt. Vision, Marin Co.				
	410-2	12_{II}	. . .	94	532
fig. 53	471	12_{II}	. . .	98	552
	613	12_{II}	. . .	95	530

TABLE 5. Chromosome Number and Cytological Behavior in Natural Taxa in *Ceanothus* (continued)

Species	Source	Chromosome Number	Chiasma Frequency	Percentage Normal Pollen	Grains Counted
	Cerastes (continued)				
C. greggii	Cuyamaca Lake,				
var. *perplexans*	San Diego Co.				
fig. 54	921	12_{II}	. . .	. . .	. . .
C. jepsonii	Mt. Tamalpais,				
	Marin Co.				
fig. 55	576	12_{II}	1.35	. . .	. . .
	627-9	. . .	. . .	93	423
	627-14	. . .	. . .	95	523
C. jepsonii	Camp Meeker,				
	Sonoma Co.				
	472	12_{II}	. . .	. . .	. . .
C. jepsonii	Knoxville,				
var. *albiflorus*	Napa Co.				
fig. 56	409-1	12_{II}	1.33	98	519
	409-3	. . .	. . .	92	541
	Highway 20 at Napa,				
	Lake Co. Line				
	598-1	12_{II}	. . .	90	504
C. masonii	Bolinas Ridge,				
	Marin Co.				
	A	12_{II}	. . .	98	517
fig. 57	564-1	12_{II}	. . .	92	722
	564-2	12_{II}	. . .	89	604
C. megacarpus	Santa Catalina				
	Island				
fig. 58	916	12_{II}	. . .	. . .	. . .
C. prostratus	2 mi N of Cobb				
var. *occidentalis*	Post Office,				
	Lake Co.				
fig. 59	597	12_{II}	. . .	94	528
	Cobb Valley,				
	Lake Co.				
	614	12_{II}	1.29	95	525
C. pumilus	Cummings,				
	Mendocino Co.				
fig. 60	485	12_{II}	. . .	94	579
C. purpureus	Summit of Wooden				
	Valley Grade,				
	Napa Co.				
fig. 61	408-23	12_{II}	. . .	96	560
	408-28	12_{II}	. . .	91	501

TABLE 5. Chromosome Number and Cytological Behavior in Natural Taxa in *Ceanothus* (concluded)

Species	Source	Chromosome Number	Chiasma Frequency	Percentage Normal Pollen	Grains Counted
		Cerastes (concluded)			
C. ramulosus	Mt. Tamalpais, Marin Co.				
fig. 62	500-1	12_{II}	...	93	450
C. ramulosus var. *fascicularis*	Pozo Mts., San Luis Obispo Co.				
fig. 63	Kamb 1617	12_{II}	...	...	...
C. rigidus	Huckleberry Hill, Monterey Co.				
fig. 64	611	12_{II}	...	94	450
	612	12_{II}	...	96	526
C. sonomensis	Trinity Mt., Sonoma Co.				
fig. 65	481-1	12_{II}	...	97	755

distinct interkinesis with the formation of a nuclear membrane and of nucleoli between telophase I and the onset of metaphase II.

An estimate of the chiasma frequency per chromosome pair at early diakinesis was made for five species, as shown in table 5. The observed frequency ranged from 1.29 to 1.37 in different species, with a mean frequency of 1.33. Usually 1 chiasma occurs on each major arm of a chromosome pair. The four larger chromosome pairs with medium centromeres generally have 2 chiasmata per pair, and the eight smaller pairs generally have 1 chiasma each. No chromosome pair with more than 2 chiasmata has been observed

Chromosome pairing in intersectional hybrids. Of the five intersectional hybrids known at present in *Ceanothus*, two have been studied cytologically and three have been limited to the examination of pollen as listed in table 6. In both hybrids studied cytologically, meiosis was highly irregular. For example, in the spontaneous hybrid X*C*. *james roof*, a product of *C*. *purpureus* (section *Cerastes* × *C*. sp. (probably *C*. *thyrsiflorus* of section *Euceanothus*), the number of chromosome pairs observed at metaphase I varied from 3 to 12, with a mean number of 8.30 per pollen mother cell, as indicated in table 7. A minimum chiasma frequency of 0.69 per chromosome pair was estimated for the hybrid in metaphase I. The chromosomal distribution at anaphase I and II was highly irregular, with scattered and lagging univalents which formed varying numbers and sizes of micronuclei at telophase II (figs. 66 to 71).

TABLE 6. Meiotic Chromosome Behavior in Intersectional Hybrids

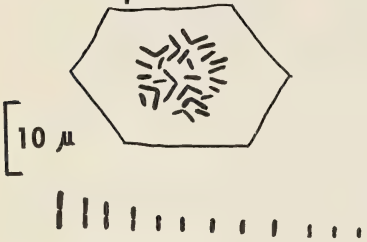
Hybrid	Chromosome Pairs at Metaphase I	Chiasma Frequency	Percentage Stainable Pollen	Grains Counted
C. purpureus (*Cerastes*)				
× *C.* sp. (*Euceanothus*)				
482 X*C. james roof*				
figs. 66 to 71	3 to 12	0.69	8	538
C. masonii (*Cerastes*)				
× *C. foliosus* (*Euceanothus*)				
414-2				
figs. 72-77	1 to 11	0.58	0	650
C. prostratus (*Cerastes*)				
× *C. velutinus* (*Euceanothus*)				
X*C. rugosus*				
U.C. no. 452524	. . .	. . .	0	738
U.C. no. 449589	. . .	. . .	0	522
C. prostratus (*Cerastes*)				
× *C. cordulatus* (*Euceanothus*)				
X*C. serrulatus*				
U.C. no. 555546	. . .	. . .	3	631
C. rigidus (*Cerastes*)				
× *C. griseus* (*Euceanothus*)				
X*C. veitchianus*				
U.C. no. 83338	. . .	. . .	1	639

The pollen from this intersectional hybrid was also highly variable in size. A questionable 8 per cent of the grains stained normally, but they had 2 to 4 times the volume of normal *Ceanothus* pollen and were probably polyploid.

The second intersectional hybrid studied cytologically was *C. masonii* × *C. foliosus*. This plant was dug in its natural habitat at Bolinas Ridge, Marin County, together with a number of seedlings of the two parental species that had germinated during the spring of 1947 after a fire. This hybrid differed cytologically from X*C. james roof* only in that fewer chromosome pairs were formed, as shown in figures 72 to 77. The minimum chiasma frequency was approximately 0.58 per chromosome pair, and no stainable pollen was observed.

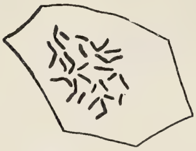
EUCEANOTHUS

thyrsiflorus var. repens



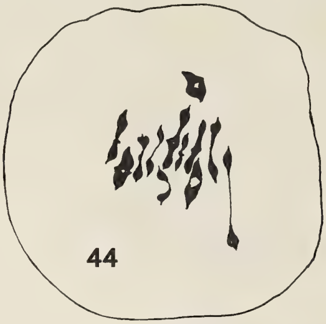
42

parvifolius N 924



43

impressus N 919



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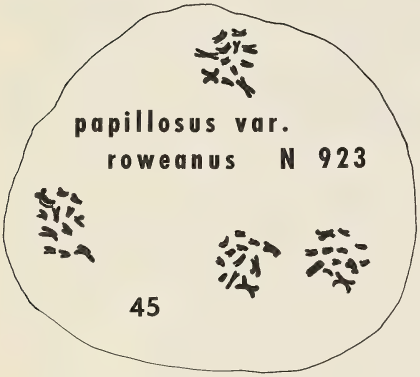
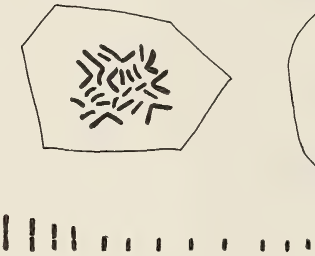
CERASTES

papillosus var. roweanus N 923



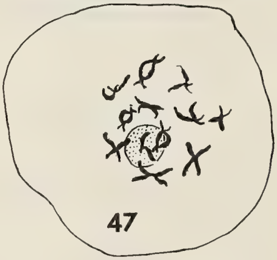
45

gloriosus B



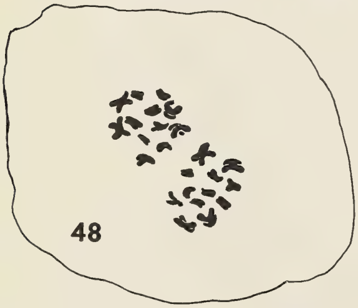
46

confusus N 608



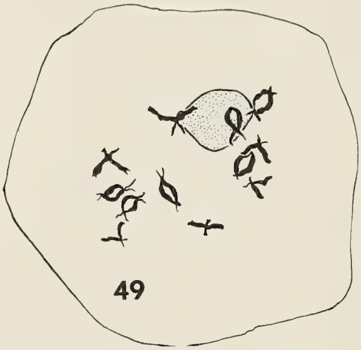
47

crassifolius N 915



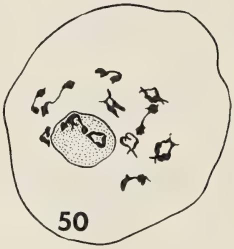
48

divergens N 477



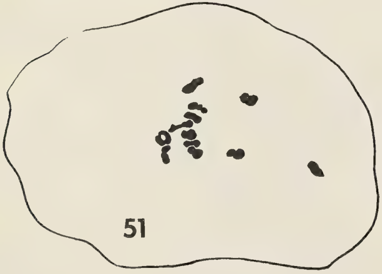
49

gloriosus B



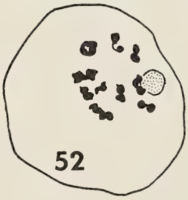
50

gloriosus N 615



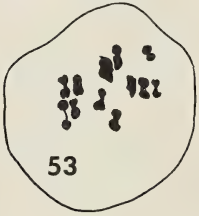
51

gloriosus var. exaltatus N578



52

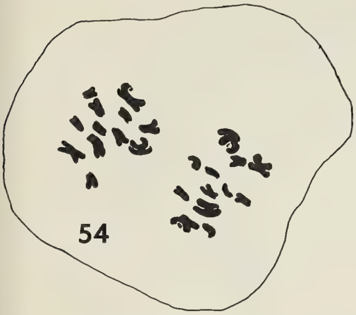
gloriosus var. porrectus N 471



53

Figs. 42-65. Somatic and meiotic chromosome plates of Euceanothus. Figs. 42, 43, and 46 Camera lucida drawings.

greggii var. perplexans N 921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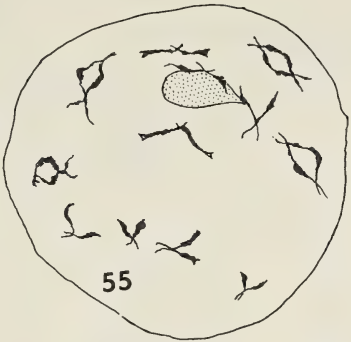
jepsonii N 576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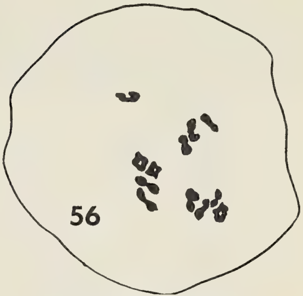
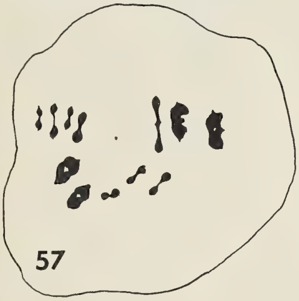
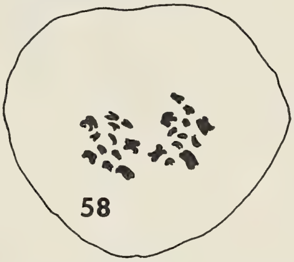
jepsonii var. albiflorus N 409-1


56

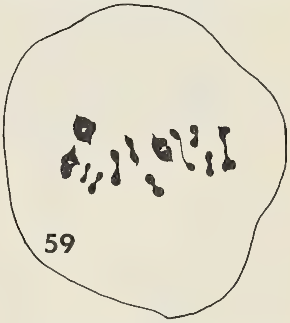
masonii N 564-1


57

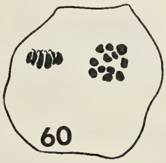
megacarpus N 916


58

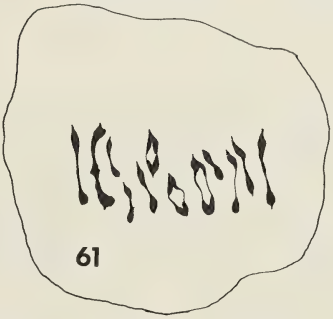
prostratus var. occidentalis N 597


59

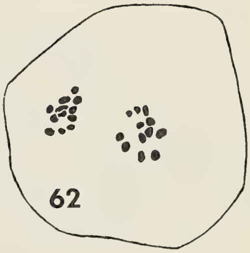
pumilus N 485


60

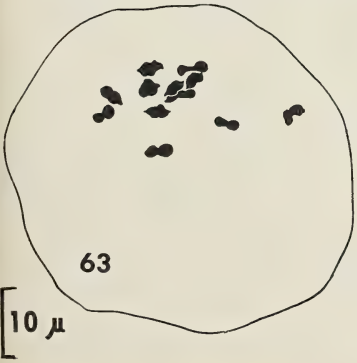
purpureus N 408-23


61

ramulosus N 500-1


62

ramulosus var. fascicularis K 1617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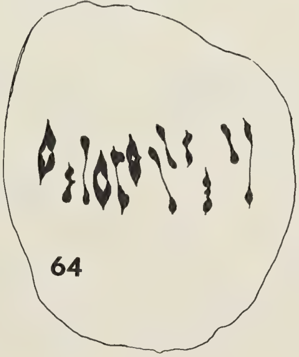
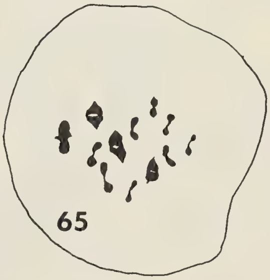
rigidus N 611


64

sonomensis N 418-1


65

10 µ

are from sectioned material; the others are from acetocarmine smear preparations. See table 5 and text.

TABLE 7. Frequencies of Bivalents per Pollen Mother Cell in Intersectional Hybrids Observed at Metaphase I

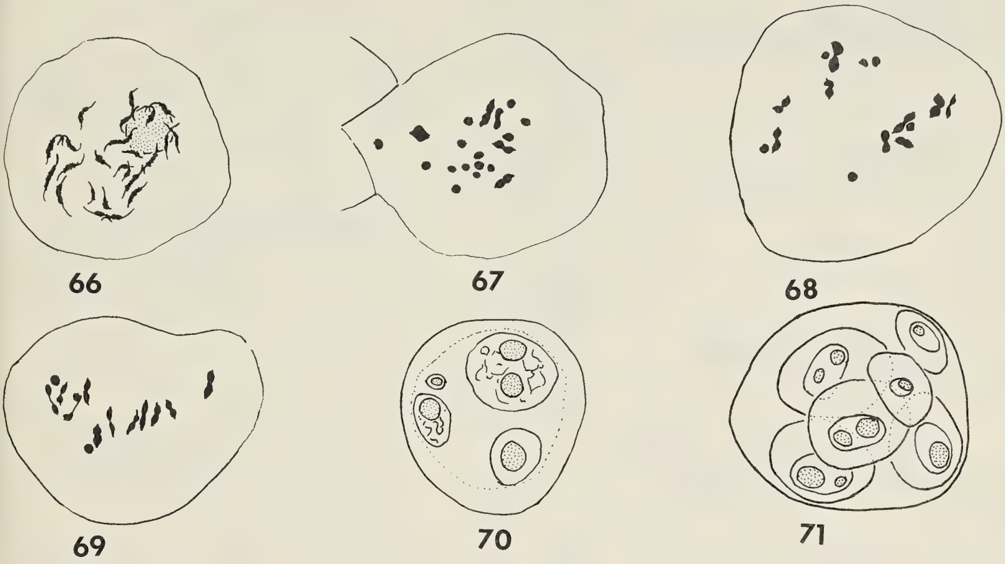
Hybrid	X*C. james roof* 482	*C. masonii* × *C. foliosus* 414-a
0_{II}	...	...
1_{II}	...	...
2_{II}	...	1
3_{II}	1	2
4_{II}	3	9
5_{II}	8	14
6_{II}	7	14
7_{II}	13	18
8_{II}	15	25
9_{II}	20	15
10_{II}	21	4
11_{II}	11	1
12_{II}	1	...
Total counts	100	102
Mean number of pairs per pollen mother cell	8.30	6.96

Pollen analysis of the three other intersectional hybrids revealed that abnormalities similar to those described above develop during reduction divisions. The pollen varied widely in size in all three hybrids. In particular, the pollen of *C. prostratus* var. *laxus* × *C. cordulatus* (X*C. serrulatus* McMinn) and of *C. rigidus* × *griseus* (X*C. veitchianus* Hook.) included abnormally large grains like those found in the hybrid X*C. james roof*.

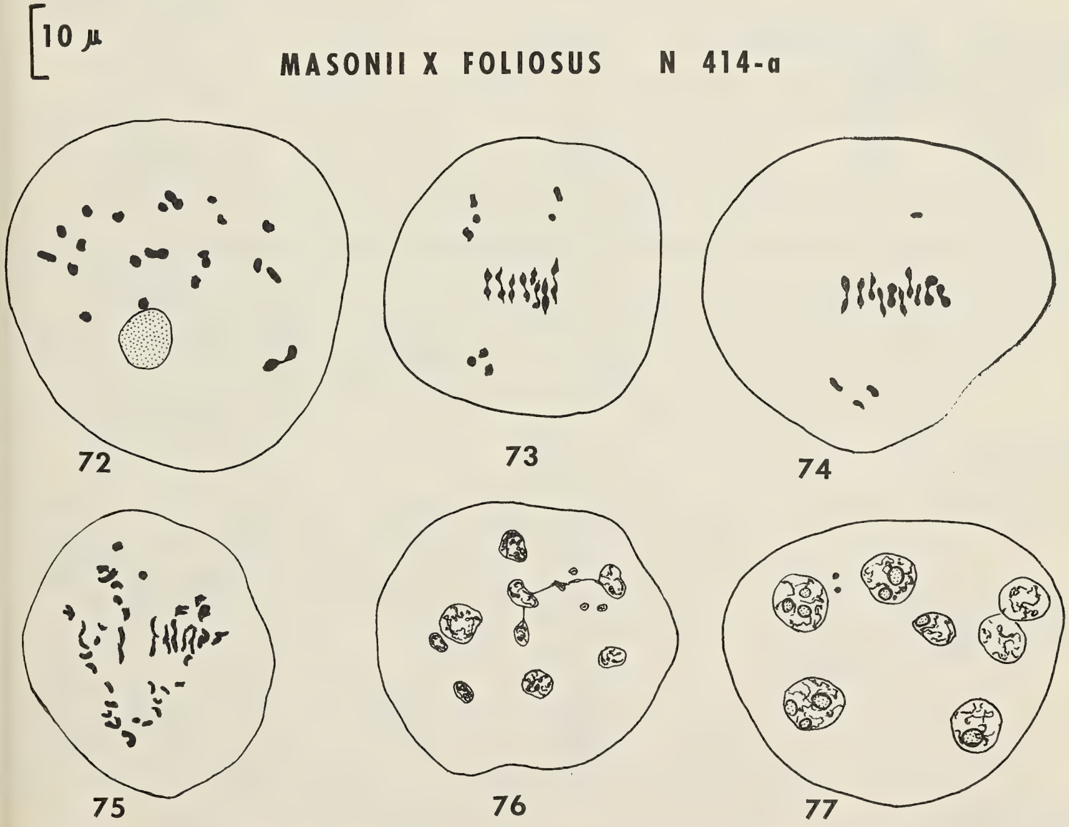
Reduction divisions in the embryo sac have not been observed; it is believed, however, that they must also be highly irregular, resulting in very low seed production. Repeated attempts to backcross the parental species with the hybrid X*C. james roof* and *C. masonii* × *C. foliosus* have been unsuccessful.

Interspecific field hybrids within section Cerastes. McMinn (1942, 1944) reported the work of the present author on the chromosome pairing of six field hybrids between species within section *Euceanothus*, and one interspecific hybrid within section *Cerastes*. All but one of these hybrids exhibited 12 chromosome pairs, showing no irregularities in the meiotic cycle. One plant from a hybrid swarm between *C. cordulatus* Kell. and *C. velutinus* Douglas had the normal 12 chromosome pairs plus an additional very small pair of chromosomes and 3 fragments. This may well be an unusual condition, for, in another hybrid from

X C JAMES ROOF



MASONII X FOLIOSUS N 414-a



Figs. 66-77. Chromosome behavior and distribution during meiotic divisions in intersectional Ceanothus hybrids.

TABLE 8. Meiotic Chromosome Behavior in Interspecific Field Hybrids Section *Cerastes*

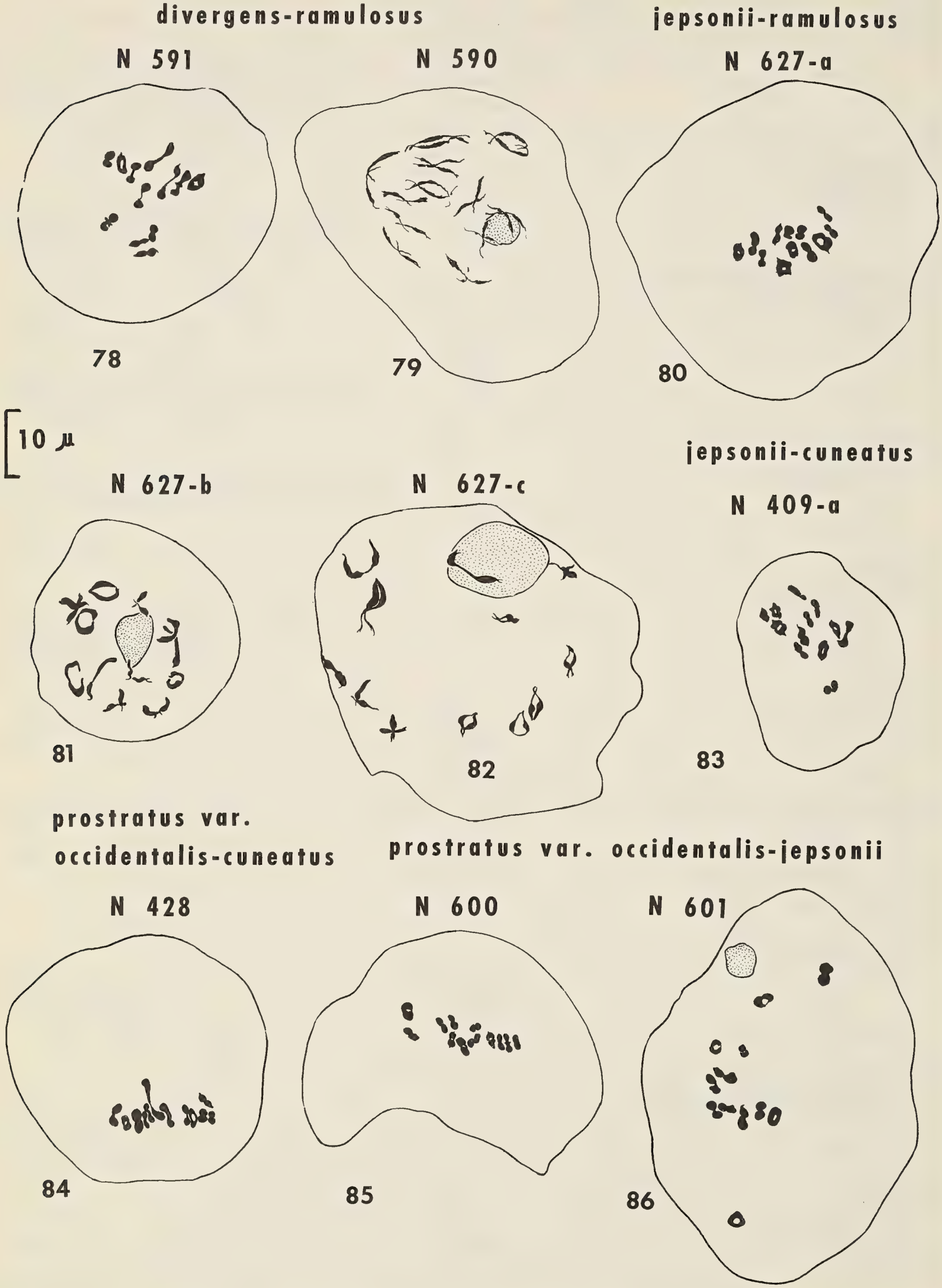
Hybrid		Chromosome Pairing	Chiasma Frequency	Percentage of Normal Pollen	Grains Counted
C. divergens-ramulosus					
Franz Valley School, Sonoma Co.					
fig. 78	591	12_{II}	. . .	95	658
fig. 79	590	12_{II}	1.31	97	755
C. jepsonii-ramulosus					
Bootjack Camp, Mt. Tamalpais, Marin Co.					
fig. 80	627-a	12_{II}	. . .	97	502
fig. 81	-b	12_{II}	1.36	96	594
fig. 82	-c	12_{II}	1.30	94	502
C. jepsonii var. *albiflorus-cuneatus*					
Knoxville, Napa Co.					
fig. 83	409-a	12_{II}	. . .	95	637
C. prostratus var. *occidentalis-cuneatus*					
Whispering Pines, Cobb Mountain, Lake Co.					
fig. 84	428	12_{II}	. . .	90	515
	429	. . .	. . .	94	511
C. prostratus var. *occidentalis-jepsonii* var. *albiflorus*					
Table Mountain, Napa Co.					
fig. 85	600	12_{II}	. . .	97	517
fig. 86	601	12_{II}	. . .	90	526

TABLE 9. Meiotic Chromosome Behavior in Controlled Interspecific Hybrids Section *Cerastes*

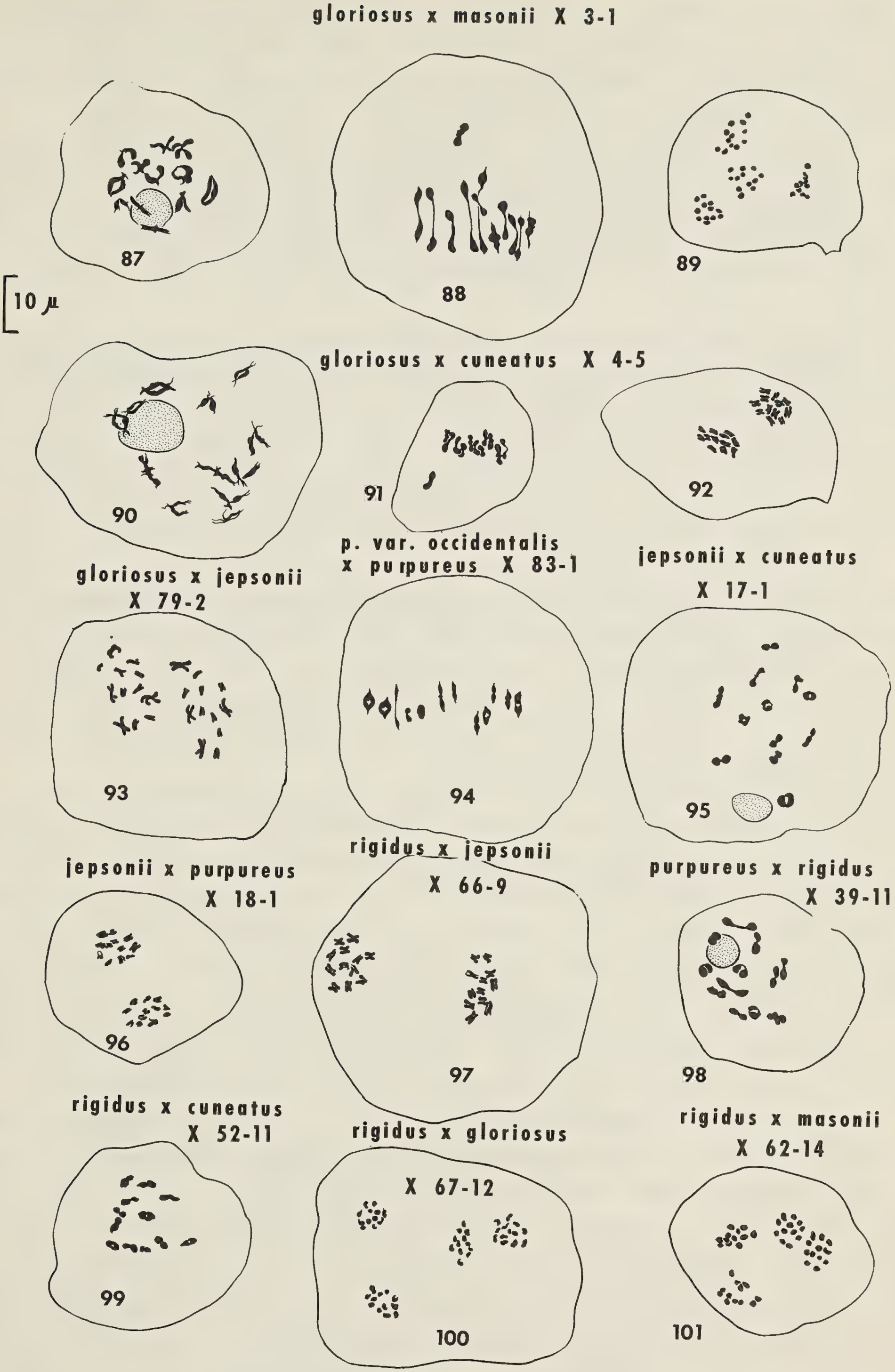
Hybrid		Chromosome Pairing	Chiasma Frequency	Percentage of Normal Pollen	Grains Counted
C. gloriosus × *C. masonii*					
figs. 87-89	X 3-1	12_{II}	1.31	88	580
	-2	12_{II}	1.30	93	689
	-3	. . .	. . .	97	640
C. masonii × *C. gloriosus*					
	X 10-1	12_{II}	. . .	92	546
	-2	12_{II}	1.33	88	520
	-3	12_{II}	1.31	88	520
	-5	12_{II}	. . .	97	622
C. gloriosus × *C. cuneatus*					
	X 4-4	12_{II}	. . .	96	530
figs. 90-92	-5	12_{II}	1.31	94	545

TABLE 9. Meiotic Chromosome Behavior in Controlled Interspecific Hybrids Section *Cerastes* (concluded)

Hybrid	Chromosome Pairing	Chiasma Frequency	Percentage of Normal Pollen	Grains Counted
C. gloriosus				
× *C. jepsonii*				
fig. 93 X 79-2	12_{II}	. . .	92	540
-6	12_{II}	. . .	94	545
C. prostratus var. *occidentalis*				
× *C. purpureus*				
X 83-1	12_{II}	. . .	89	462
-20	12_{II}	. . .	95	530
-24	12_{II}	1.29	97	520
fig. 94				
C. jepsonii				
× *C. cuneatus*				
X 17-1	12_{II}	. . .	95	460
fig. 95				
C. jepsonii				
× *C. purpureus*				
X 18-1	12_{II}	. . .	96	570
fig. 96				
C. rigidus				
× *C. jepsonii*				
X 66-9	12_{II}	. . .	91	633
fig. 97				
C. purpureus				
× *C. rigidus*				
X 39-11	12_{II}	. . .	91	633
fig. 98				
C. rigidus				
× *C. cuneatus*				
X 52-11	12_{II}	. . .	94	401
-12	12_{II}	. . .	98	447
fig. 99				
C. rigidus				
× *C. gloriosus* var. *porrectus*				
X 67-12	12_{II}	. . .	97	429
fig. 100				
C. rigidus				
× *C. masonii*				
X 62-14	12_{II}	. . .	94	290
fig. 101				



Figs. 78-86. Meiotic chromosome behavior in interspecific field hybrids, section *Cerastes*.


gloriosus x masonii X 3-1
87
88
89
10 µ
gloriosus x cuneatus X 4-5
90
91
92
gloriosus x jepsonii X 79-2
p. var. occidentalis x purpureus X 83-1
jepsonii x cuneatus X 17-1
93
94
95
jepsonii x purpureus X 18-1
rigidus x jepsonii X 66-9
purpureus x rigidus X 39-11
96
97
98
rigidus x cuneatus X 52-11
rigidus x gloriosus X 67-12
rigidus x masonii X 62-14
99
100
101

Figs. 87-101. Chromosome behavior and distribution in reduction divisions of controlled interspecific F_1 hybrids, section *Cerastes*.

the same swarm, normal meiosis with 12 chromosome pairs was observed. The pollen fertility for two other plants from this swarm also indicates that their meiosis was regular: in one plant 96 per cent of the pollen among 710 grains was found to be normal, and in the other 95 per cent among 572 grains.

During the present work nine additional field hybrids between taxa within section *Cerastes* have been studied, as indicated in table 8 and figures 78 to 86. Meiosis was regular in all. Normal chromosome pairs with regular distribution at anaphase I and II were found consistently. Chiasma frequency, when studied, and pollen stainability did not drop below the range exhibited by the parental species.

Chromosome pairing in controlled interspecific hybrids within section Cerastes. A selected sample of 21 first-generation hybrids covering ten different interspecific combinations all showed normal meiosis with 12 pairs of chromosomes; see table 9 and figures 87 to 101. The chiasma frequency, when determined, was found to be only slightly reduced as compared with that in the parental species, and the percentage of stainable pollen and of seed set was also within the range of that found in the parental species.

Conclusions. The available evidence indicates that *Ceanothus* is a homoploid genus like *Quercus* (H. J. Sax, 1930; Duffield, 1940; Darlington and Wylie, 1956) and *Pinus* (K. Sax and H. J. Sax, 1933), and that polyploidy, if existing at all, is exceedingly rare and has not been an important factor in speciation within the genus. Reproductive isolation between section *Euceanothus* and section *Cerastes* is apparently complete. The rare intersectional hybrids that have been found have proved to be completely sterile.

The data presented here agree with the conclusions of McMinn (1942 and 1944) that the genus is composed of two distinct cenospecies which correspond with the sections *Euceanothus* and *Cerastes* that are incapable of gene interchange. Within each section, however, there are few sterility barriers between the recognizable species. This is particularly true for members of section *Cerastes* occurring in the north coast range, the group of species that has been studied in greatest detail. No irregularities in chromosome pairing were noted in any of these interspecific hybrids. The chiasma frequency, when determined, was found to be only slightly less than that in the parental species, and the percentage of "good" pollen likewise fell well within the normal range.

The cytogenetic situation within the sections of *Ceanothus* appears to be quite comparable to the now classic example of *Aquilegia* (Clausen, Keck, and Hiesey, 1945; Munz, 1946; Stebbins, 1950; and Grant, 1952). In this genus, as within the sections of *Ceanothus*, the chromosome number is constant (with the exception of a few polyploids) and, on the cytogenetic level, isolating barriers between the described species are few or weak. Here, as in the section *Ceanothus*, vastly diverse forms have evolved that probably maintain their identity through complex physiological isolating mechanisms, including highly sensitive selection in different local environments independent of chromosomal or genic compatibility.

CHAPTER III

FIELD STUDIES

In order to evaluate the cytogenetic observations in relation to the variation pattern found under natural conditions, a limited geographical area was selected for detailed field study. It included approximately 7500 square miles in the north coast ranges consisting of a strip slightly more than 50 miles wide and extending for about 150 miles from San Francisco Bay (latitude 38°N) north to a point a little south of Cape Mendocino (latitude 40°N). Eleven of the twenty-two species recognized by McMinn (1942) in section *Cerastes* are represented in this area.

Physiographic features of the study area. The region is one of low mountainous relief dissected by a series of cultivated valleys which run in general from north to south. The elevation extends from sea level and slightly above in the interior valleys to several peaks over 6000 feet, and many points on intervening mountain ridges rise to more than 3000 feet.

The climate is mild and, like that of the rest of California, is characterized by distinct wet and dry seasons. The wet season extends from about September to June, with precipitation mostly in the form of rain, although some snow lies for short periods upon higher mountains. There is a general gradient from high rainfall in the northwestern part of the region, with 54 inches or more per year at Willits, Mendocino County, to a lower rainfall area in the southeastern part at Napa, which has approximately 23 inches per year. The transition is by no means regular, for the varied topography imposes a complicated pattern of local variation. Along the coast and in the interior valleys fogs are frequent throughout the year, both augmenting the precipitation and reducing total evaporation.

The temperatures throughout the region are never severe. A gradient exists from the coast, with a typical maritime condition having little diurnal or seasonal fluctuation, to a semicontinental climate in the interior, where the daily fluctuations are much larger and seasonal extremes range from above 100°F in the summer to below 20° F during the winter.

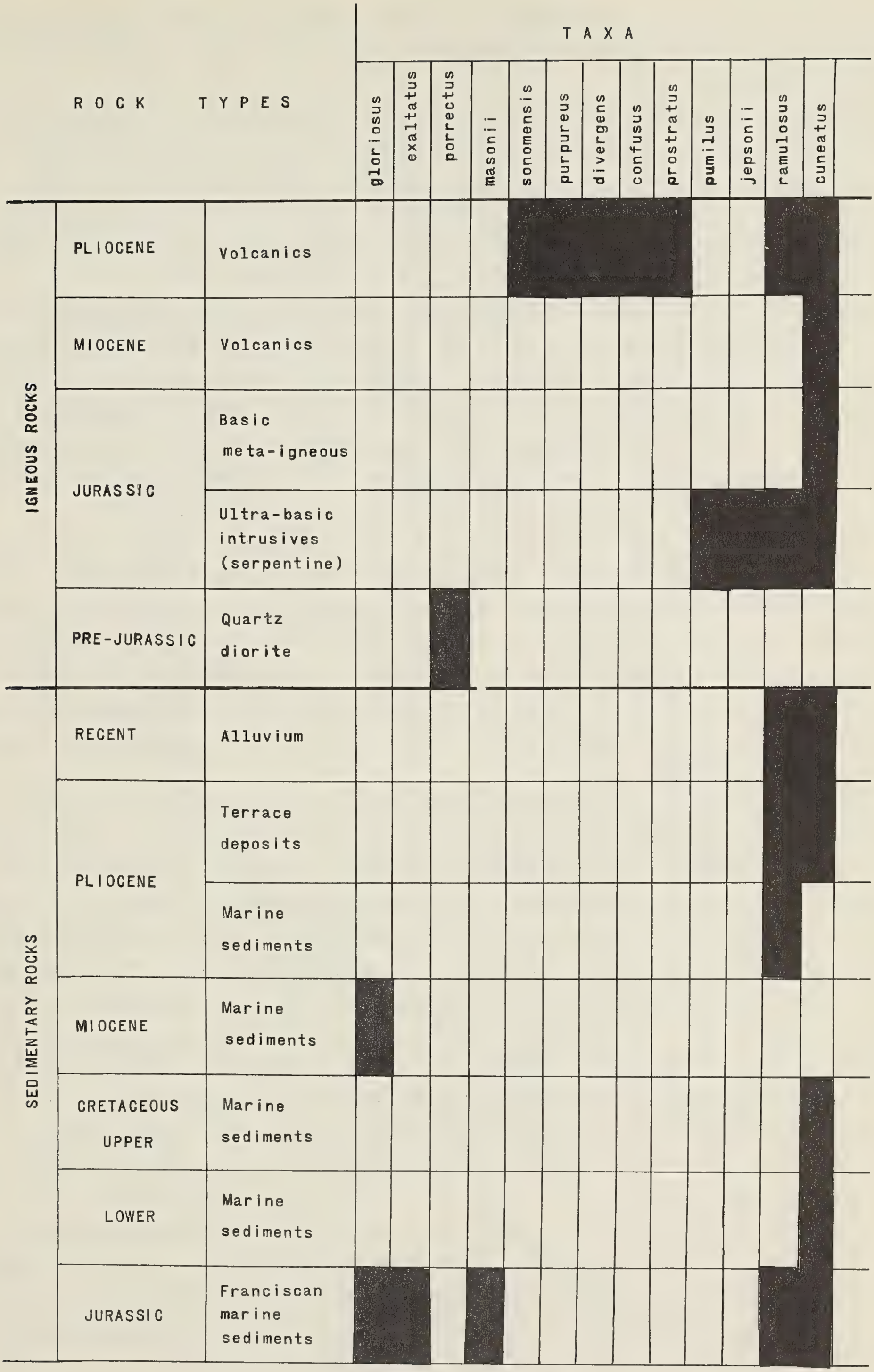
The most variable aspect of the region is the geology (Ostmont, 1905; Reed, 1933; Jenkens, 1938; Taliferro, 1934; Mason, 1946a and b; Weaver, 1949; Kruckeberg, 1951). Basically it is supported by Franciscan sediments, which are generally believed to be of Jurassic or early Cretaceous age. This is only the foundation matrix that encloses or supports a great array of geological formations. The southeastern part of the area is dominated by a cap of Pliocene volcanic materials composed of a complex series of lava flows, tuff beds, obsidian, and ash deposits which are occasionally interspersed with gravels and conglomerates. In the north and west the Franciscan series dominates. This is a complex group of sedimentary beds, ranging from sandstones (dominant) to conglomerates, shales, foraminiferous limestones, and radiolarian cherts. Contemporaneous flows of basalt and diabase, as well as extensive intrusions of highly mineralized basic igneous rocks that later became serpentinized, are frequent. During past geological ages faulting and erosion have exposed this complex array, which has, with weathering, given rise to a highly differentiated group of local soil types.

The importance of the edaphic factor in the distribution of plant species has been recognized clearly (Morrison, 1941; Mason, 1946a and b; Kruckeberg, 1951; Jowett, 1959; Bradshaw, 1960; Bradshaw, Lodge, Jowett, and Chadwick, 1960). This factor appears to be of major importance in the distribution and population dynamics of the various members of section Cerastes represented in this area.

Figure 102 portrays the species of Ceanothus represented in the study area, and the geological formations upon which each is found. It is evident from this figure that the entities represented fall into two groups. First are the species that are restricted to special edaphic conditions derived from a particular type of rock. Included here are C. jepsonii, C. pumilus, C. prostratus var. occidentalis, C. confusus, C. purpureus, C. sonomensis, and C. masonii. With the exception of C. prostratus and C. pumilus, all these taxa are endemic to this immediate area and are restricted to local and specialized habitats. Ceanothus jepsonii is the most striking example of this, and, although it is found in discontinuous populations nearly throughout the area, all populations are restricted to serpentine soils.

The other group of species is distinguished from the first category in being able to occupy a much wider range of edaphic conditions. Ceanothus cuneatus and C. ramulosus, which exhibit the broadest range of tolerance, occur in semicontinuous populations on nearly all soil types within their range. Ceanothus gloriosus, although found predominantly on Franciscan sandstones, occurs also on Miocene sediments and Recent alluvia which have mixed origin derived from both the Franciscan series and lower Pliocene volcanics. The variety porrectus occurs on pre-Jurassic quartz diorite.

Methods. Population samples were taken and field studies were made at strategic localities within the area. A limited series of samples was also taken from species that have representatives in geographical regions outside the area described above in order to evaluate variation both within and between the taxa represented. These samples consisted of one flowering branch from the upper part of each plant taken at random from thirty to fifty mature individuals in each population. If the number of individuals in a particular population was less than thirty, all mature individuals were represented. The samples were then



ROCK TYPES			TAXA												
			gloriosus	exaltatus	porrectus	masonii	sonomensis	purpureus	divergens	confusus	prostratus	pumilus	jepsonii	ramulosus	cuneatus
IGNEOUS ROCKS	PLIOCENE	Volcanics					■	■	■	■	■			■	■
	MIOCENE	Volcanics													■
	JURASSIC	Basic meta-igneous													■
		Ultra-basic intrusives (serpentine)										■	■	■	■
	PRE-JURASSIC	Quartz diorite			■										
SEDIMENTARY ROCKS	RECENT	Alluvium												■	■
	PLIOCENE	Terrace deposits												■	■
		Marine sediments												■	
	MIOCENE	Marine sediments	■												
	CRETACEOUS UPPER	Marine sediments													■
	LOWER	Marine sediments													■
	JURASSIC	Franciscan marine sediments	■	■		■								■	■

Fig. 102. Summary of the geological formations upon which the taxa in section Cerastes are found in the north coast ranges of California.

preserved as herbarium specimens for further study. In areas where collecting was restricted, data were obtained directly in the field; they are here referred to as "field census."

In the study of the samples, vegetative and inflorescence characters were most helpful, because comparable information could be obtained from all individuals represented within the population sample. Characters of the fruit, although highly diagnostic, could not readily be used, because in unfavorable years fruits are formed on only a few scattered plants within a population or not at all over large areas.

Group I. The members of this group include *Ceanothus cuneatus* (Hook.) Nutt., *C. ramulosus* (Greene) McMinn, *C. sonomensis* J. T. Howell, *C. masonii* McMinn, and *C. gloriosus* J. T. Howell. These are treated together because they appear to be somewhat arbitrary segments of one large intergrading series between the extremes, *C. cuneatus* and *C. gloriosus*, which are conspicuously distinct morphologically. Figure 103 indicates the localities from which the various population samples have been obtained, as listed in table 10.

Ceanothus cuneatus is found on dry hills and ridges at lower elevations from Mexico north into Oregon. It occurs as a semicontinuous population in the more arid eastern part of the area. *Ceanothus gloriosus* is found in discontinuous populations, the typical form on coastal bluffs, and its variety *exaltatus* in the mesic chaparral in the fringes of redwood forests where fogs are frequent. Between these two extremes a large number of highly variable populations occur, which intergrade morphologically and include the taxa *C. ramulosus*, *C. sonomensis*, and *C. masonii*.

Distinguishing characters of group I. The leaf shape in mature plants of the extremes, *C. cuneatus* and *C. gloriosus*, is strikingly different. The angle of departure of veins from the midrib is a readily measurable character that accurately portrays this difference. The cuneate-spatulate leaves of *C. cuneatus* are characterized by an acute angle between veins and midrib; the relatively broader angle between midrib and veins in *C. gloriosus* reflects their broadly elliptic to nearly orbicular form. To standardize this measurement, the angle formed by the second vein from the leaf base and the midrib on the right side of the lower surface of one characteristic leaf of each specimen was measured. Figure 104 graphically represents the variation found both within and between the population samples as one progresses from east to west (bottom to top) across the area, as well as the similarity of the experimental hybrid populations to the intermediate taxa.

The leaf margin in mature plants also provides a readily determinable character. *Ceanothus cuneatus* generally has entire leaves, only exceptional plants in a population having one or two small marginal leaf dentations; in contrast, *C. gloriosus* has highly dentate leaf margins. The number of dentations on the same leaves as in the study above was used to represent this character. Its variation pattern is represented in figure 105.

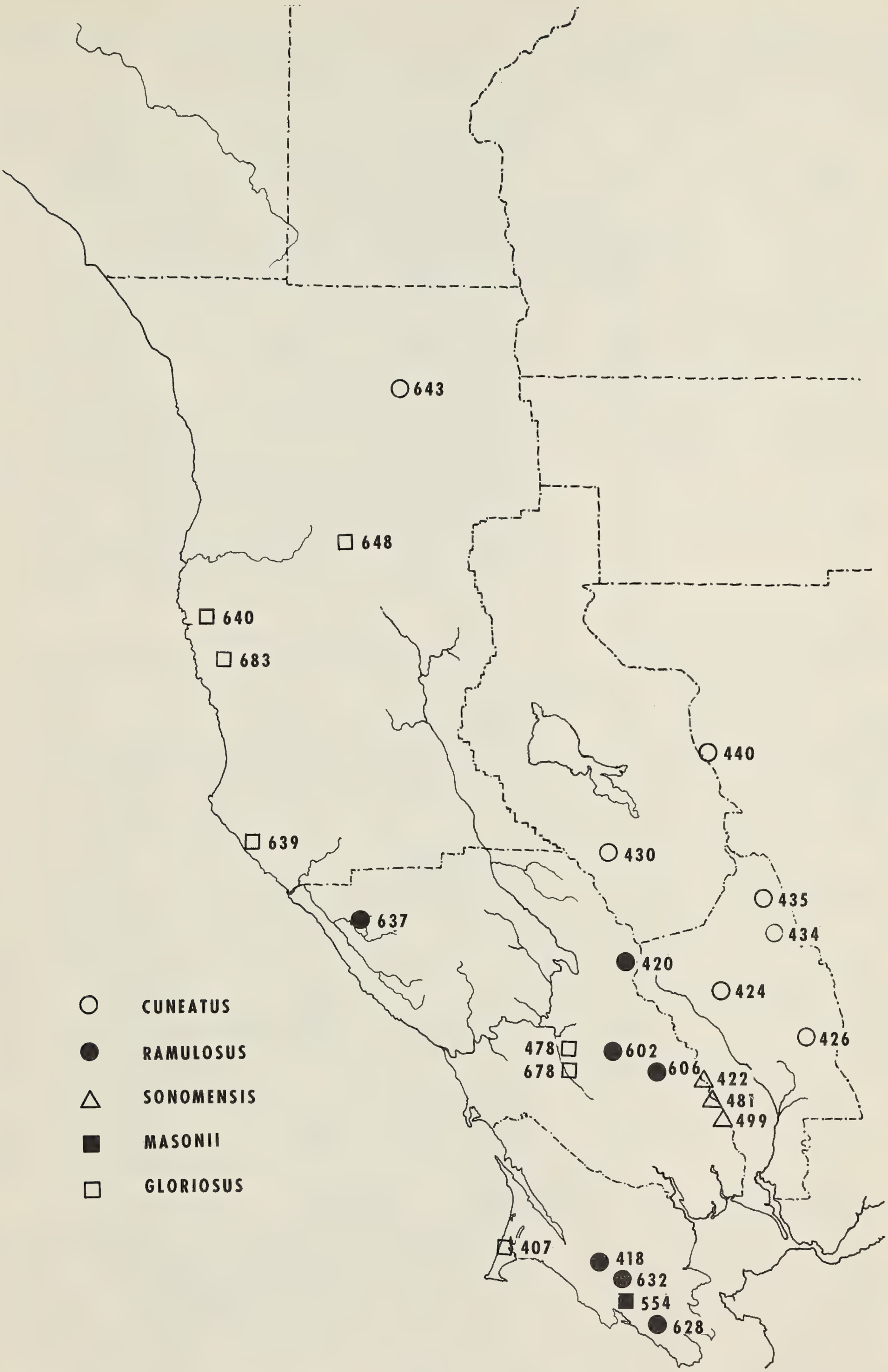


Fig. 103. Localities of sampled field populations of the Ceanothus cuneatus-gloriosus series.

TABLE 10. Localities and Number of Individuals Represented in Population Samples for the *Ceanothus cuneatus-gloriosus* Series

Sample Number	Number of Individuals	Source
		Ceanothus cuneatus
753*	31	Cliff House, Tuolomne Co., Sierra Nevada
458*	30	Rock Creek, Nevada Co., Sierra Nevada
516*	19	Slate Creek, Shasta Co., Klamath Mts.
426	13	10 miles south of Monticello, Napa Co.
434	35	2 miles south of Knoxville, Napa Co.
435	27	Knoxville, Napa Co.
440	30	Wilbur Springs, Colusa Co.
643	31	Covelo, Mendocino Co.
424	34	Howell Mt., Napa Co.
430	26	Cobb Mt., Lake Co.
		C. ramulosus†
420	31	Franz Valley School, Sonoma Co.
606	31	Hope Valley, Sonoma Co.
602	23	1 mile east of Santa Rosa, Sonoma Co.
637	24	7 miles southeast of Annapolis, Sonoma Co.
628	15	Mt. Tamalpais, Marin Co.
418	31	Lagunitas, Marin Co.
632	31	Carson Creek, Marin Co.
		C. sonomensis
422	31	Trinity Mt., Sonoma Co.
481	31	2.5 miles north of Buena Vista, Sonoma Co.
499	31	Hooker Canyon, Sonoma Co.
555	21	Trinity Mt. grown in U.C. Botanical Garden, Berkeley
		C. masonii
554‡	30	Bolinas Ridge, Marin Co.
414	13	Seedlings from Bolinas Ridge grown in U.C. Botanical Garden, Berkeley
646	11	Seedlings from Bolinas Ridge grown in Mills College Test Garden, Oakland, by McMinn
647	8	Seedlings from Bolinas Ridge grown by L. L. Edmonds at Danville, Contra Costa Co.
		C. gloriosus
639§	31	Anchor Bay, Mendocino Co.
407	35	Point Reyes, Marin Co.
		C. gloriosus var. *exaltatus*
678¶	34	Vine Hill, Sonoma Co.
478	18	1 mile northwest of Sebastopol, Sonoma Co.
648	31	5 miles north of Willits, Mendocino Co.
638	32	6 miles east of Albion, Mendocino Co.
640	31	Mendocino City Airport, Mendocino Co.
		Hybrid Cultures
		C. gloriosus × *C. cuneatus*
X4 F_1	4	Point Reyes × northern Napa Co.
X100 and 101 F_2	34	Point Reyes × northern Napa Co.

TABLE 10. Localities and Number of Individuals Represented in Population Samples for the *Ceanothus cuneatus-gloriosus* Series (concluded)

Sample Number	Number of Individuals	Source
		C. masonii × *C. gloriosus*
X10 F_1	4	Bolinas Ridge × Point Reyes
X110 F_2	43	Bolinas Ridge × Point Reyes

*Populations obtained outside the area and separated from any other member of section *Cerastes*.

†Reference to *C. ramulosus* in this paper is restricted to the forms north of San Francisco Bay. Experimental and field studies not yet complete on the forms south of San Francisco Bay indicate that these forms have a parallel origin, but that the variations are derived from *C. rigidus* rather than *C. gloriosus* through introgression.

‡Type, McMinn 3044, included for reference.

§Type, J. T. Howell 242192, included for reference.

¶Type, J. T. Howell 194492, included for reference.

The stipules, as pointed out by Howell (1940a), are of considerable diagnostic importance in distinguishing species. In *C. cuneatus* they are small, entire, and erect, and ascend toward the tips of the branches of even older growth. In *C. gloriosus* the stipules are highly developed, thick, and "corky," and have fimbriate-dentate margins. They become strongly reflexed at maturity and can reach an over-all length of as much as 7 mm. The total length from the center of the base to the tip of the stipule is easily measured and was used in this study. Figure 106 represents the variation found in stipule length in the same set of specimens as treated above. Here, again, there is clinal variation between the extremes.

Qualitative characters between the extremes are equally distinct. The branchlets produced by the previous year's growth are very characteristic. The strict branches of *C. cuneatus* are smooth and round, and only rarely do they show faint traces of ridges between the nodes. The bark is covered with a thin, scaly coating of a chloroform-soluble substance, giving it a silvery gray appearance. In contrast, *C. gloriosus* has pronounced ridges extending between the nodes, the bark lacks the scaly coating, and it is generally deep maroon-red. In these characters an intergrading series also exists.

The flowers of *C. cuneatus* are creamy white and develop into dark green or brown fruit, whereas those of *C. gloriosus* range from light blue to dark blue-violet and develop correspondingly darker, maroon to black fruit. These characters again follow the same intergrading pattern in the geographically intermediate populations.

A group of five of the above-mentioned characters which showed free recombination in the experimental hybrid cultures (table 4) was chosen for study

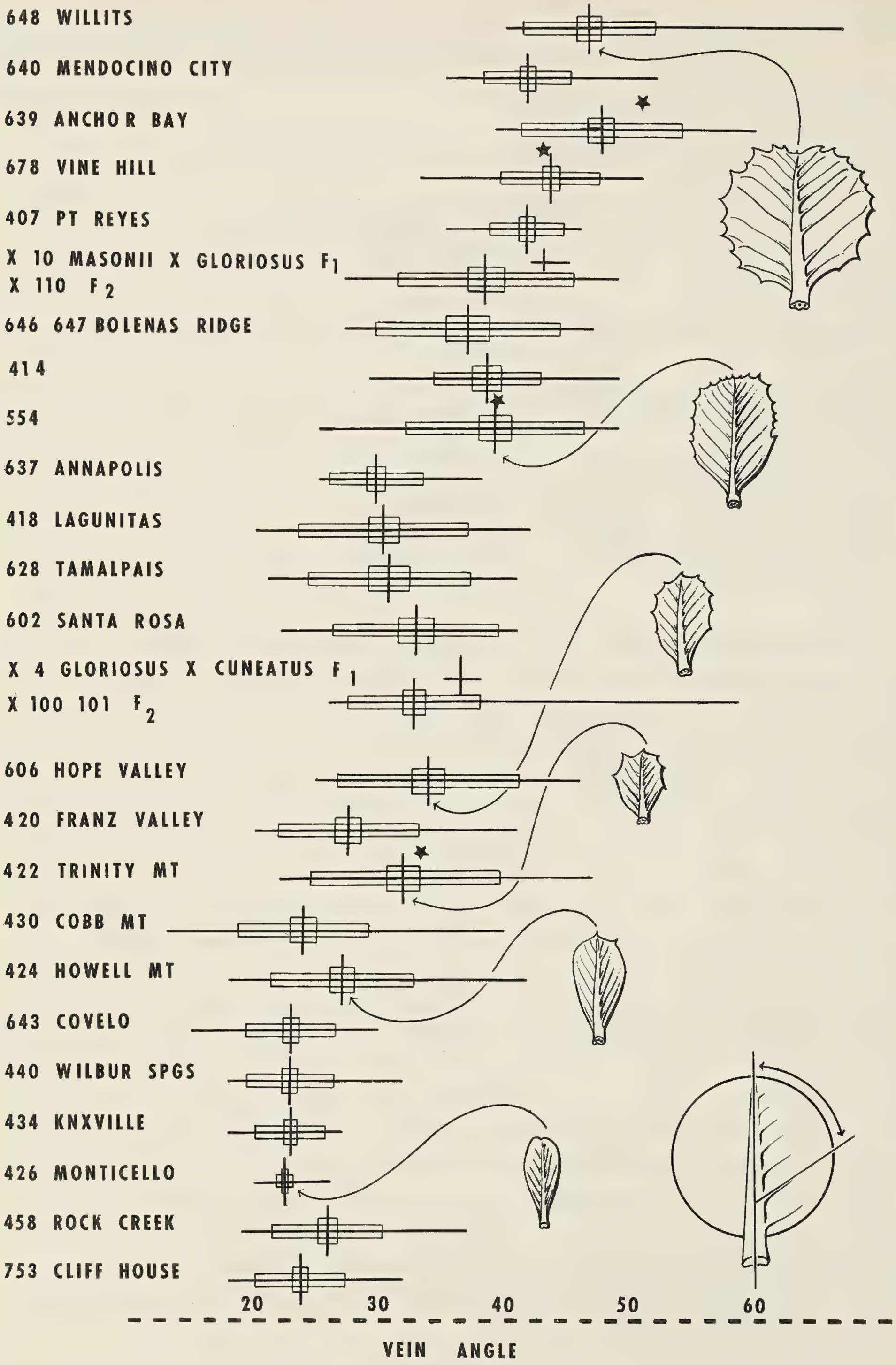
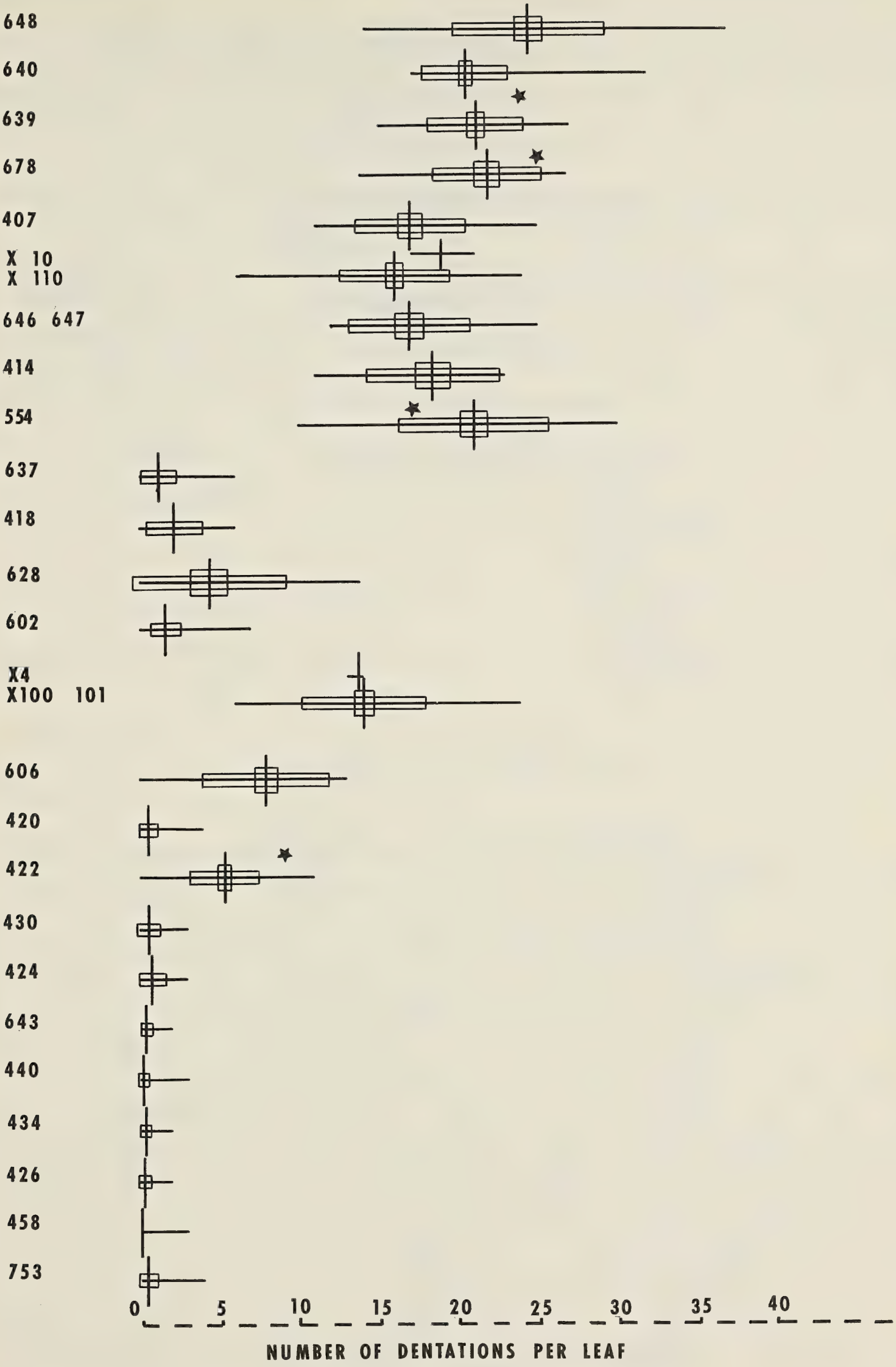


Fig. 104. Statistical summary comparing variation in angle between the midrib and veins in leaves of C. cuneatus (753, 458, 426, 434, 440, 643, 424, and 430), C. ramulosus (420, 606, 602, 628, 418, and 637), C. sonomensis (422), C. masonii (554, 414, 646, and 647), C. gloriosus (407, 678, 639, 640, and 648), and experimental hybrids (× 4, × 100, × 101, × 10, and × 110).

The long horizontal line indicates the population range, and the vertical



line the mean. The narrow open bar represents the standard deviation, and the thick open bar the standard deviation mean. Stars indicate type specimens.

Fig. 105. Variation in leaf dentation in the C. cuneatus-gloriosus series.

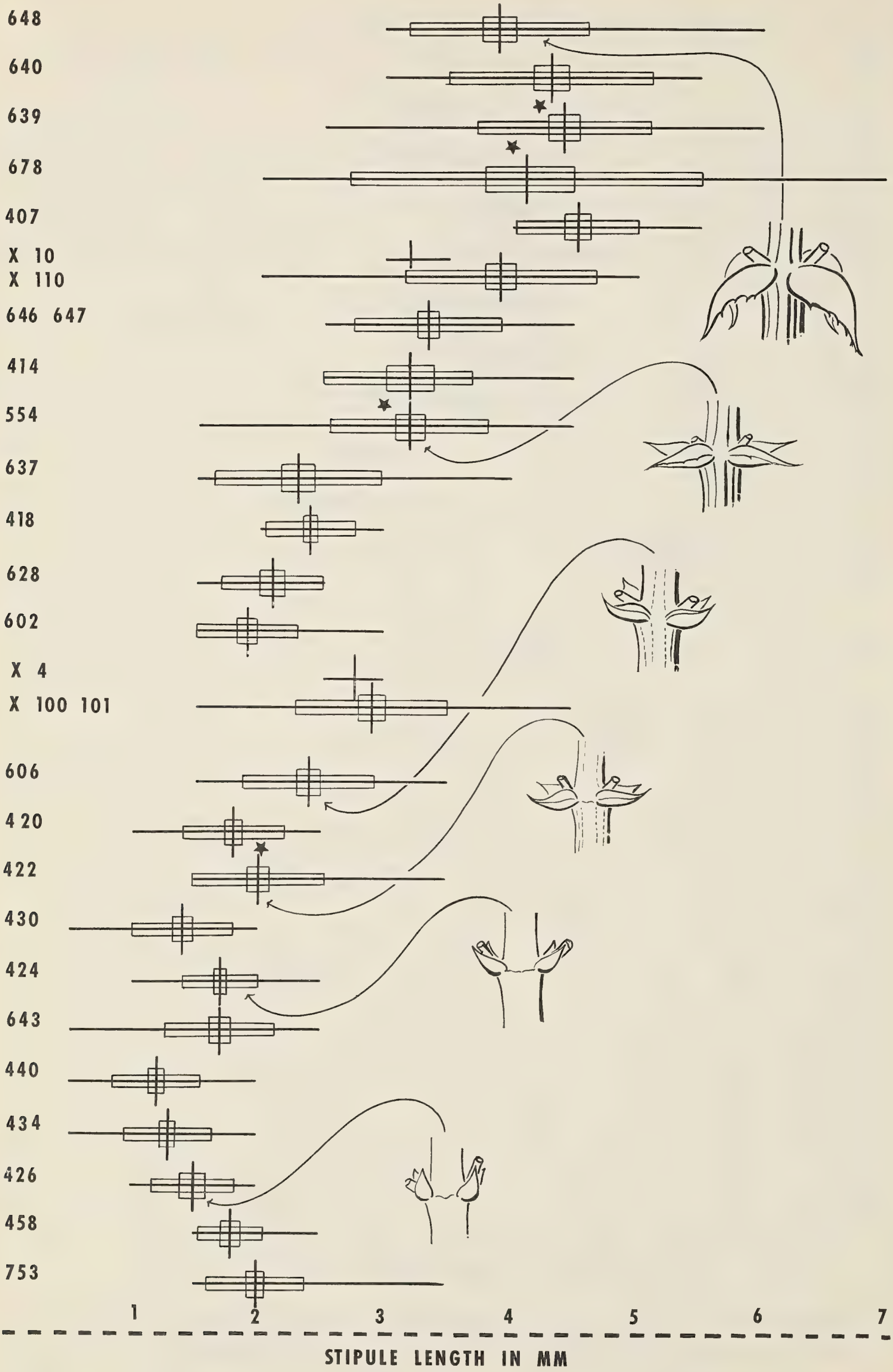


Fig. 106. Variation pattern in the stipules of the C. cuneatus-gloriosus series. See figure 104 for explanation of the graphs.

in an analysis of the population samples employing the hybrid index method of Anderson (1936). Since none of these characters exhibited dominance, all were assigned a uniform value (table 11) giving a total aggregate score of 0 for *C. cuneatus* and a total of 10 for *C. gloriosus*.

TABLE 11. Index Values for Five Character Differences between *Ceanothus gloriosus* and *C. cuneatus*

Character	*C. gloriosus*	Intermediate	*C. cuneatus*
Angle between veins and midrib in leaf	38° to 60° Value 2	31° to 37° Value 1	14° to 30° Value 0
Number of dentations per leaf margin	14 to 27 Value 2	5 to 13 Value 1	0 to 4 Value 0
Stipules	Reflexed Value 2	Intermediate Value 1	Erect Value 0
Branchlets	Strongly ridged Value 2	Intermediate Value 1	Smooth Value 0
Bark color	Maroon red Value 2	Intermediate Value 1	Silvery gray Value 0
Total index value	10	5	0

The aggregate values for each plant in each population sample are summarized in the histograms of figure 107, and, as in the individual characters, the populations sampled exhibit the same intergrading series. The populations of *C. cuneatus* from the Sierra Nevada, the Klamath Mountains, and the arid eastern part of the area show little variation. *Ceanothus gloriosus*, although somewhat more variable, forms a discrete unit in the more mesic coastal region and in the fringes of redwood forests.

In the areas between these extremes, the variation between individuals within each population is sufficient to bridge the gap between the extremes. The experimental hybrid population *C. gloriosus* × *cuneatus* offers a striking parallel with many of these intermediate populations. This is even more evident in a pictorial scatter diagram of the type used by Anderson (1949, 1954). Figure 108 depicts the variation pattern in the population of *C. gloriosus* from Point Reyes, Marin County, contrasted with *C. cuneatus* from Knoxville, Napa County, and the striking similarity between the recombinations found in the F_2 progeny of the artificial hybrid *C. gloriosus* × *cuneatus* and the natural variable population of *C. ramulosus* from Hope Valley, Sonoma County.

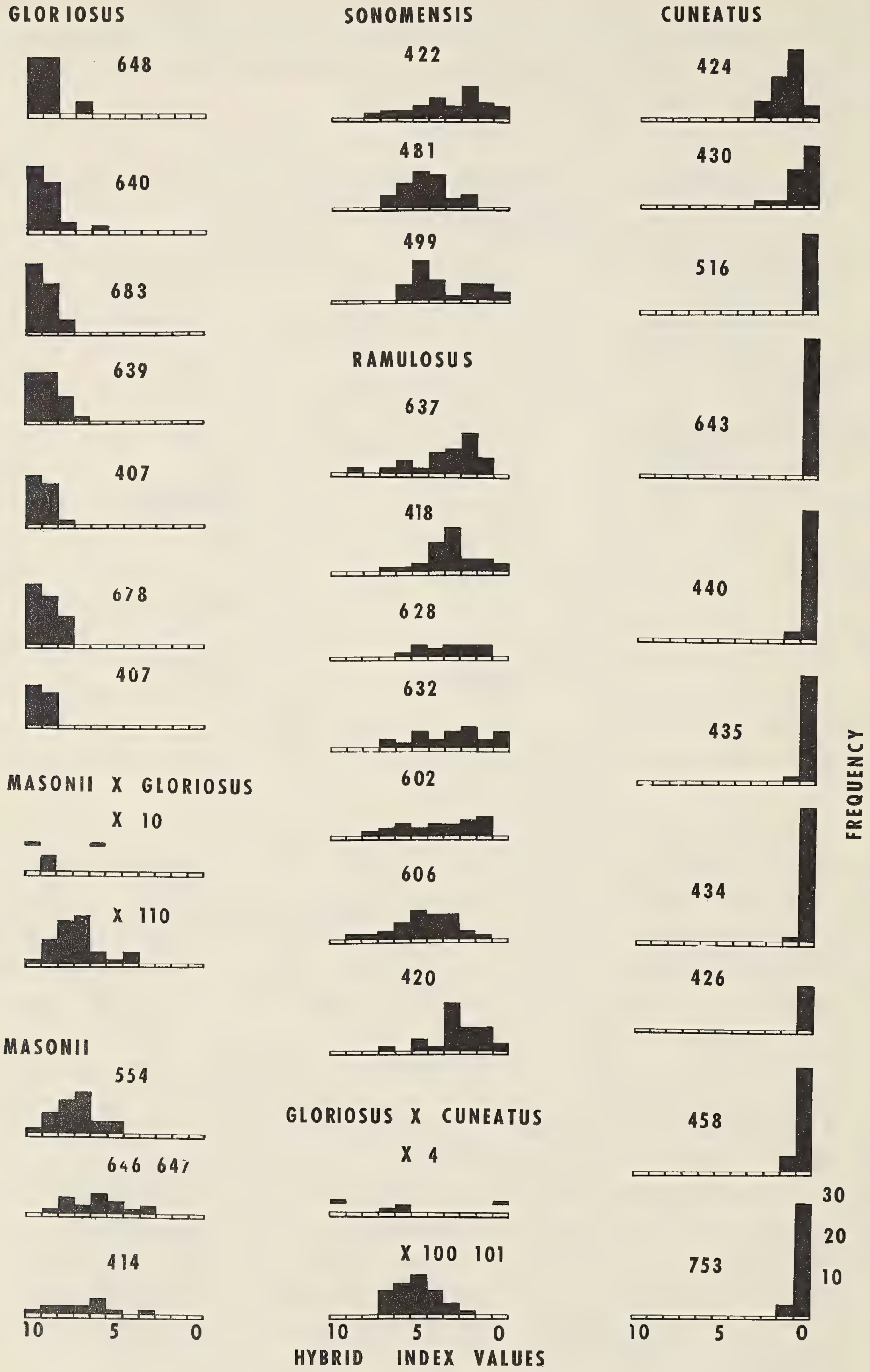


Fig. 107. Frequency distributions of index values of individual plants of population samples of C. cuneatus-gloriosus series. See table 11 for explanation of index values.

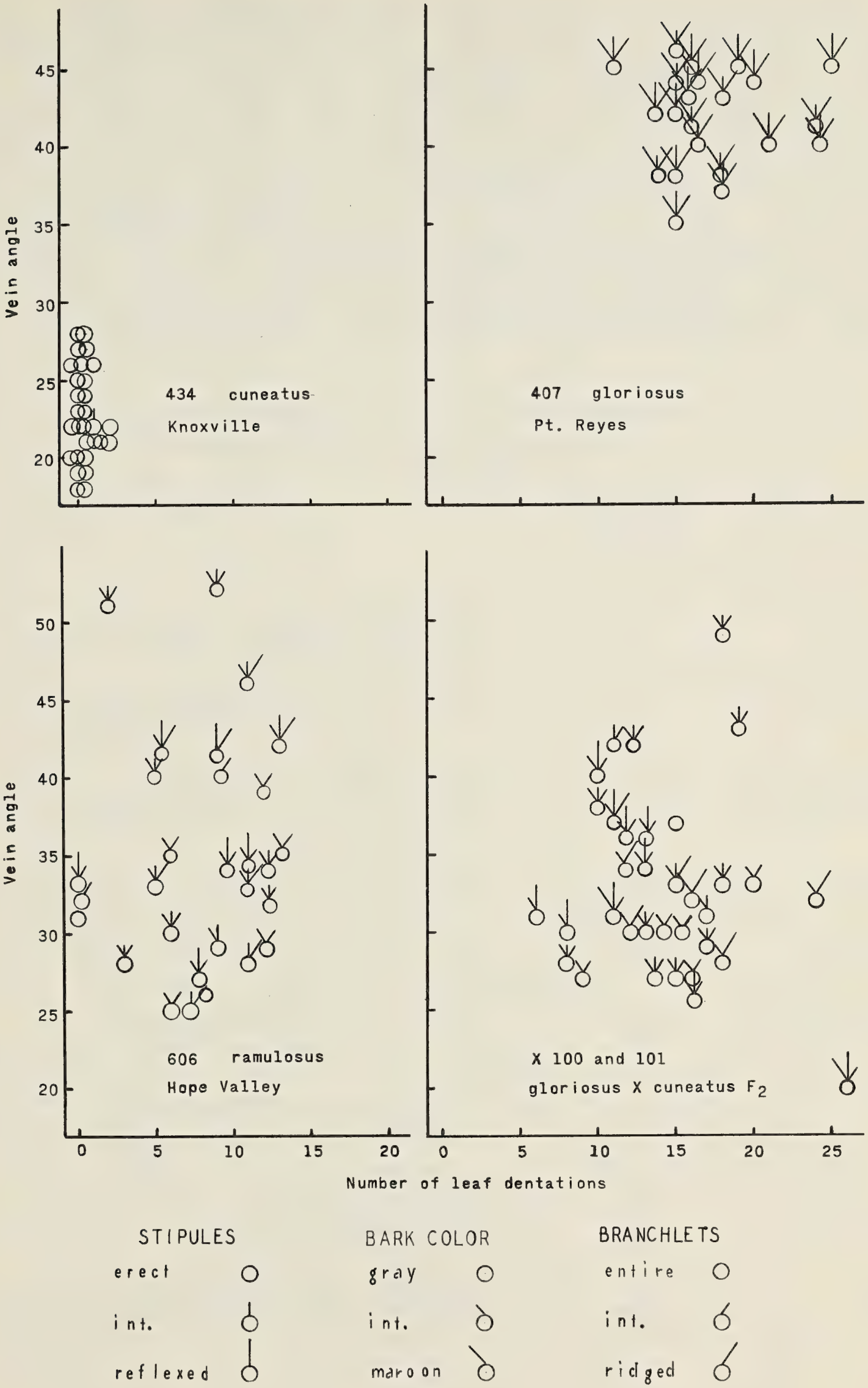
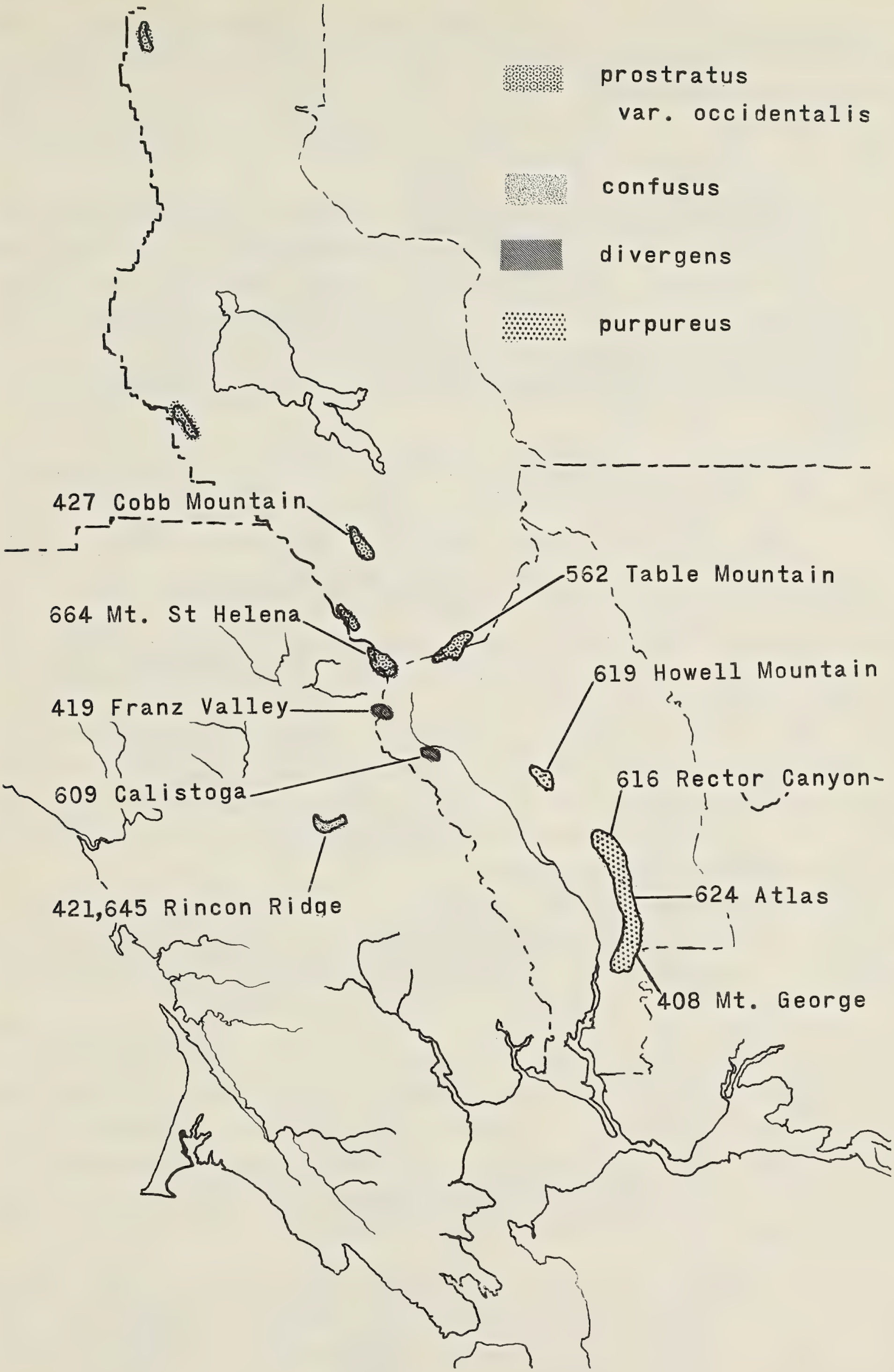


Fig. 108. Pictorialized scatter diagrams, comparing individuals of one population each of Ceanothus cuneatus, C. gloriosus, and C. ramulosus, and F_2 progeny of C. gloriosus × cuneatus.

Group II. Included in group II are *Ceanothus purpureus* Jepson, *C. divergens* Parry, *C. confusus* J. T. Howell, and *C. prostratus* var. *occidentalis* McMinn. These taxa have a pattern of variation similar to that described in group I and are therefore described here in comparable terms. Group II differs from group I in that all the taxa occur only on soils derived from Pliocene volcanics, and the geographic distributions of the taxonomic entities are extremely localized and discontinuous. The series, which has as its extremes *C. purpureus* and *C. prostratus* var. *occidentalis*, is found in the eastern part of the area with clinal variation extending from south to north. The localities from which the population samples listed in table 12 were obtained are indicated in Figure 109. Two samples of *C. prostratus* from the lower Sierra Nevada are also included for reference.

TABLE 12. Localities and Number of Individuals Represented in Population Samples for the *Ceanothus purpureus-prostratus* Series

Sample Number	Number of Individuals	Source
		C. purpureus
Nobs 408	32	Mt. George, summit of Wooden Valley grade, Napa Co.
Nobs 624	31	Atlas Hills, Napa Co.
Nobs 616	31	Rector Canyon, 4 miles east of Yountville, Napa Co.
Nobs 619	32	Southern slopes of Howell Mt., Napa Co.
		C. divergens
Nobs 419	32	Franz Valley School, Sonoma Co.
Nobs 609	25	Conner Ranch, 1 mile south of Calistoga, Napa Co.
		C. confusus
Nobs 421	31	2 miles northeast of County Farm, Rincon Ridge, Sonoma Co.
Nobs 645	31	Los Olivos Rd., Rincon Ridge, Sonoma Co.
		C. prostratus var. *occidentalis*
Nobs 664	25	Summit of Mt. St. Helena, Lake Co.
Nobs 562	29	4 miles east of Mt. Hill House on Table Mt. Rd., Lake Co.
Nobs 427	31	7 miles northeast of Cobb Post Office, Cobb Mt., Lake Co.
		C. prostratus
Nobs 666	31	Forest Ranch Butte Co.
Nobs 669	32	Grass Valley, Nevada Co.
		C. prostratus var. *occidentalis* × *C. purpureus* F_1
X83	20	Cobb Mt., Lake Co. × Atlas Hills, Napa Co.



109. Distribution of C. prostratus var. occidentalis, C. confusus, C. divergens, and C. purpureus, and localities from which population samples were obtained.

Ceanothus purpureus, as was pointed out by J. T. Howell (1939a), is probably closely related to C. gloriosus. It is a component of the arid chaparral, and grows on shallow stony soils derived from St. Helena rhyolite of the Pliocene Sonoma volcanics (as mapped by Weaver, 1949). It is found in a semicontinuous population from just southeast of Napa north to the southern slopes of Howell Mountain in Napa County.

Ceanothus prostratus var. occidentalis is found to the north in the mountains of Lake County and extends south to the northernmost part of Napa County. Like the typical form of C. prostratus, it is a ground-cover shrub in the Pinus ponderosa forests, and occurs on heavy red clay soils derived from Pliocene volcanics. Between these two, and also on Pliocene volcanic soils, is a group of small, isolated, highly variable populations which include C. divergens and C. confusus.

Growth habit has always been an important diagnostic criterion in separating these taxa. Ceanothus purpureus is an erect shrub with its tallest branches rising from 1 to 2 meters. The branches, although spreading, rarely touch the ground, and when they do no rooting takes place. On the other hand, C. prostratus var. occidentalis forms dense prostrate mats with the branchlets rarely exceeding 24 cm in height. Rooting is common whenever the branches become partly covered with soil. Within these extreme taxa the growth habit is uniform. The field sketches shown in figure 110 from the Atlas population for C. purpureus and the Grass Valley and Cobb Mt. populations for C. prostratus are typical. The geographically intermediate populations, including C. divergens and C. confusus, are highly variable; only a small segment of these vast, diverse arrays can be represented in the figure. Not only the erect as contrasted with prostrate habit but also the ability to layer under natural conditions appear to have recombined in these intermediate populations.

A measurable aspect of this diversity is the maximum height that the branches ascend from ground level. Figure 111 illustrates the variation for this character within and between the population samples listed in table 12 as one progresses from south to north (bottom to top, respectively).

Leaf shape is again reflected by venation pattern. The broad angle between veins and midrib in C. purpureus is a reliable indication of the suborbicular to broadly elliptic leaf form in this taxon, whereas the relatively more acute angle between the veins and midrib reflects the cuneate-spatulate leaf form of both C. prostratus and its variety occidentalis. The angle formed by the second vein from the base and the midrib on the right-hand side of the leaf was measured in the same manner as in the study of group I. The results of this study are summarized in figure 112.

A similar intergrading pattern is found when the number of marginal dentations per leaf is used for the same set of leaves, as shown in figure 113. The range extends between the highly dentate condition found in C. purpureus to the pentadentate or tridentate condition in C. prostratus.

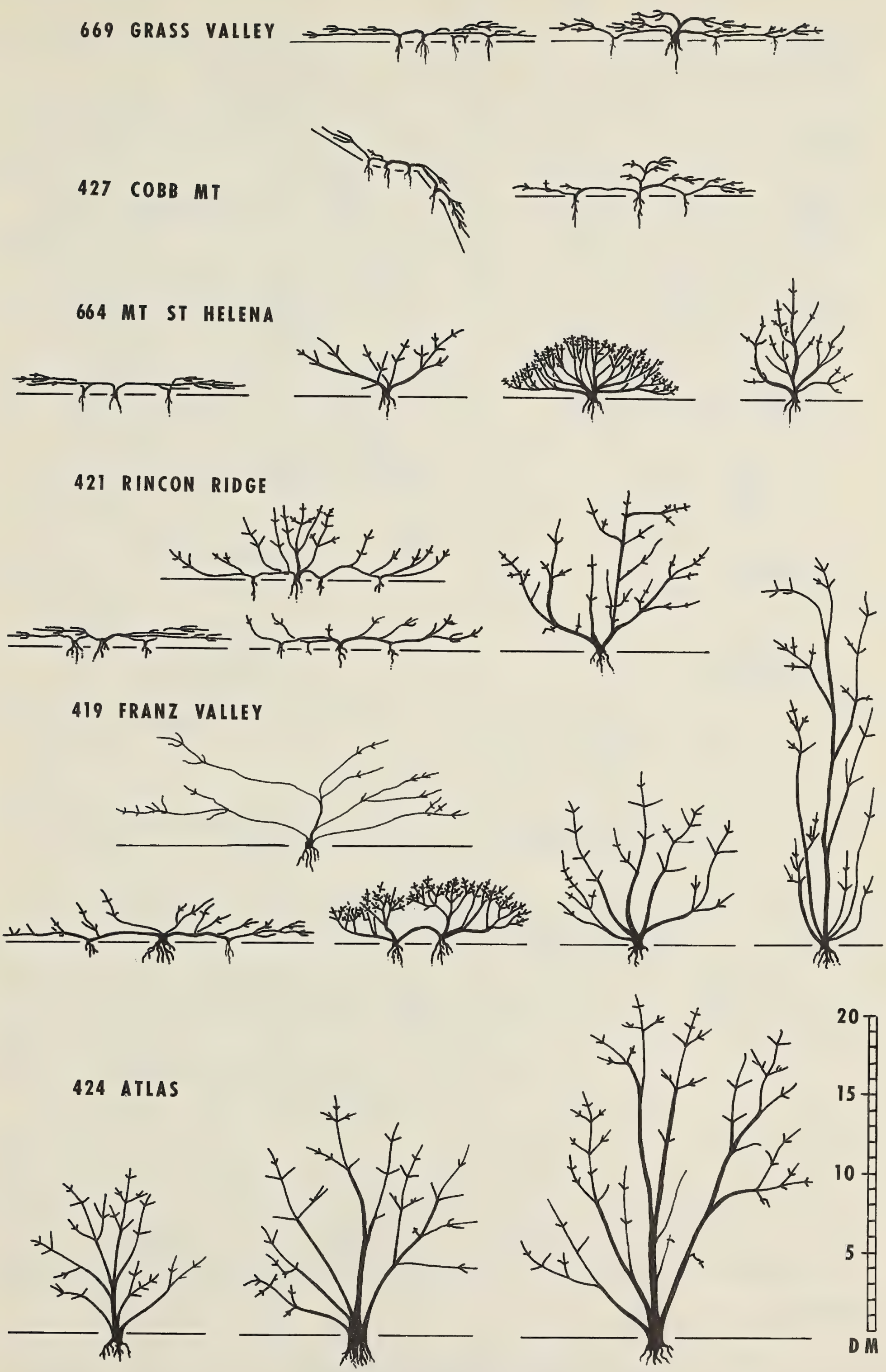


Fig. 110. Field sketches showing various habits of growth in selected populations of the C. purpureus-prostratus series.

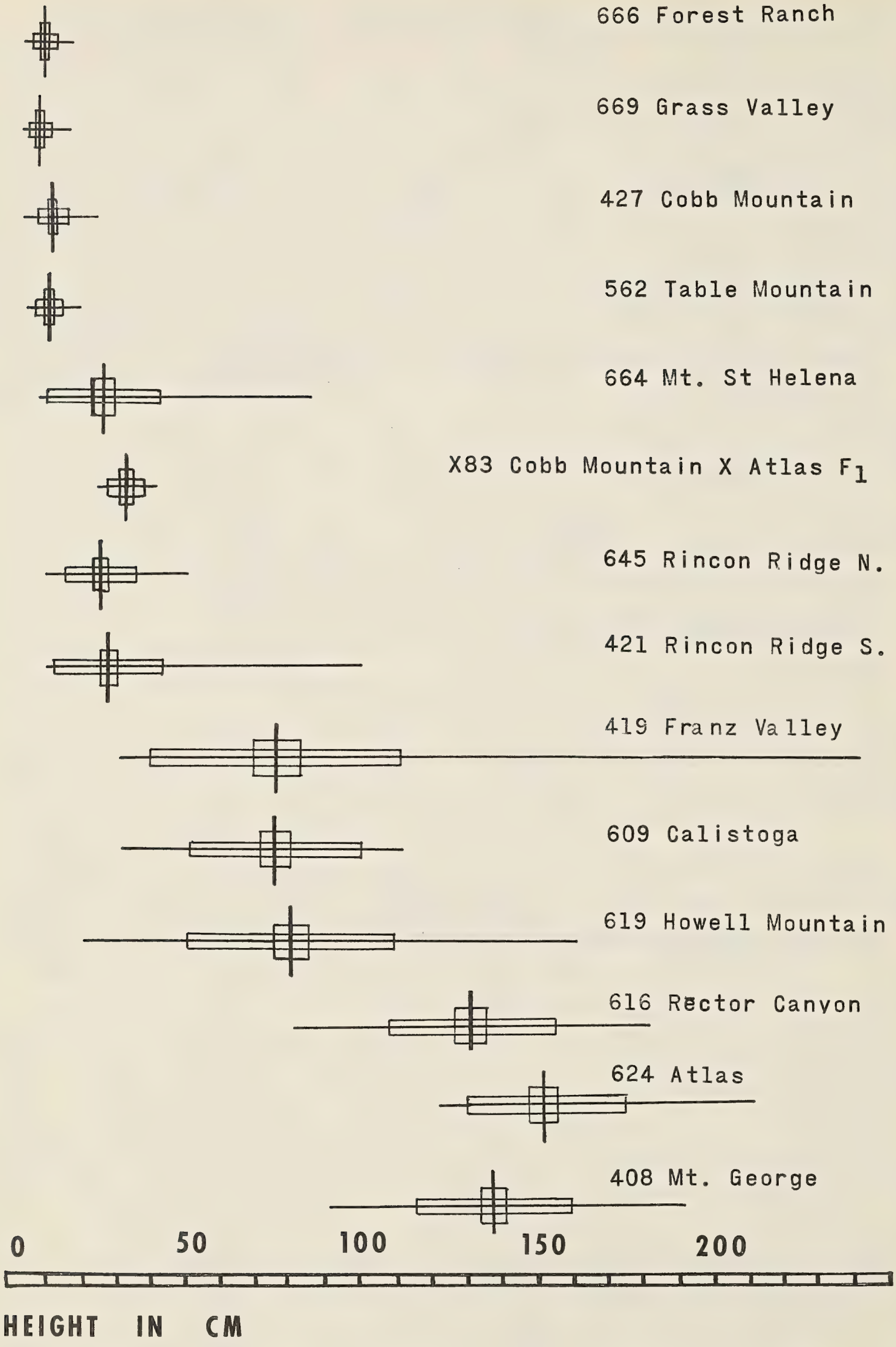
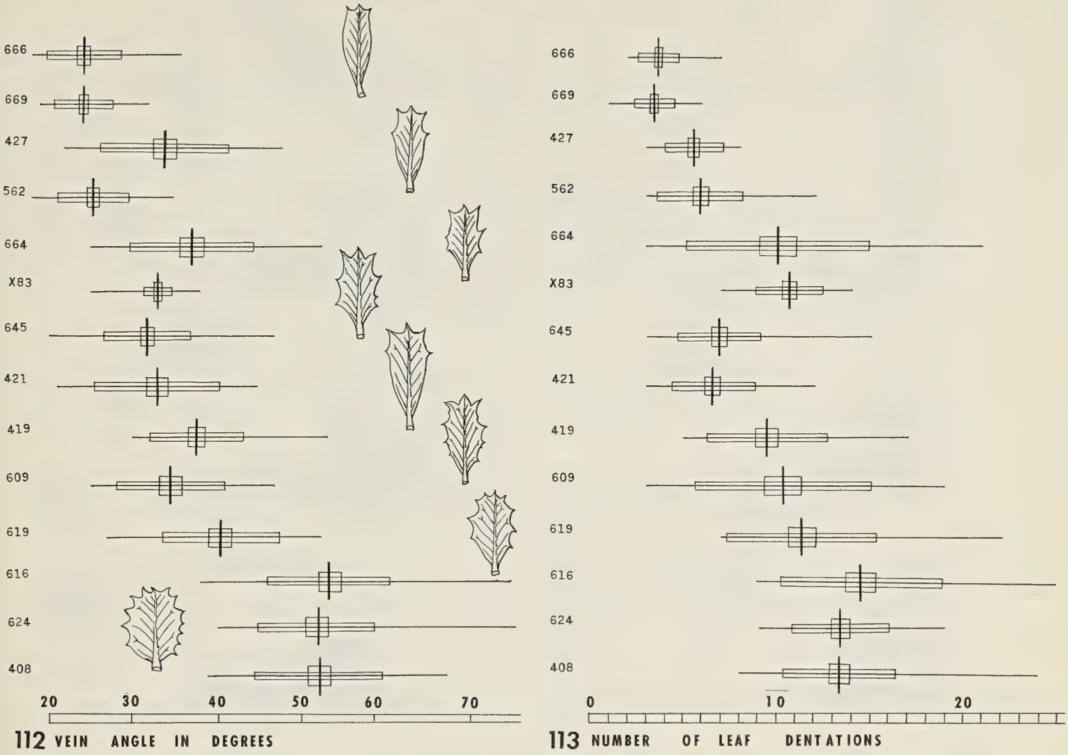


Fig. 111. Statistical summary showing variation in plant height in population samples of the C. purpureus-prostratus series. See figure 104 for explanation of the graphs.

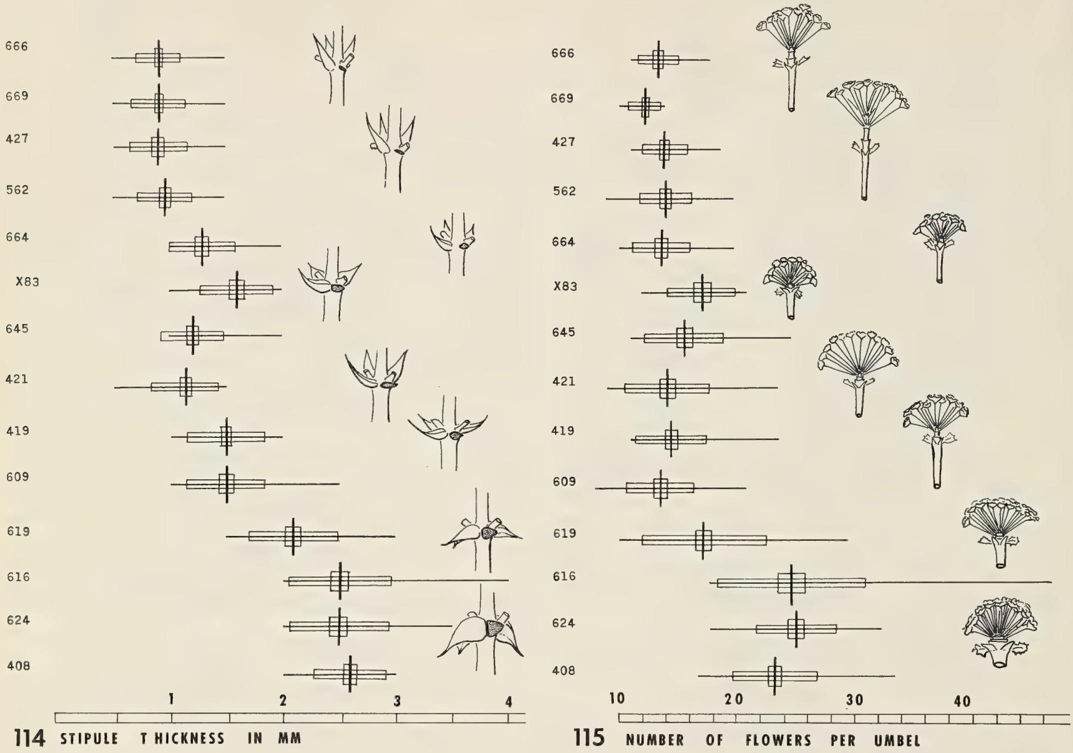


Figs. 112-113. Variation in leaf characters in the *C. purpureus-prostratus* series. See figure 104 for explanation of graphs.

The stipules are also conspicuously different in the extreme taxa. Although the stipule is elongate in both *C. purpureus* and *C. prostratus*, in *C. purpureus* it is greatly thickened and reflexed at maturity, whereas in *C. prostratus* it is thin to nearly membranous and remains erect. The width of the stipule at its base measured after removal is used to represent this character. Its intergrading pattern of variation is represented in figure 114.

The inflorescences, although umbellate throughout the section, yield additional diagnostic characters in this series of taxa. The peduncles in *C. purpureus* are stout and contracted, and bear numerous flowers in each umbel; in *C. prostratus* the peduncle is slender and elongate, and each umbel contains relatively few flowers. Figure 115 represents the variation found in number of flowers per umbel from one characteristic inflorescence of each specimen of the population samples represented.

A hybrid index study based on the five above-mentioned characters is summarized in table 13 and shown graphically in figure 116. Essentially the same pattern is evident here as in the intergrading series between *C. cuneatus* and *C. gloriosus*.



Figs. 114-115. Variation in stipule and inflorescence characters in C. purpureus-prostratus series. See figure 104 for explanation of graphs.

TABLE 13. Index Values for Five Character Differences between C. prostratus and C. purpureus

Character	C. prostratus	Intermediate	C. purpureus
Total height, centimeters	8 to 25 Value 0	26 to 99 Value 1	100 to 200 Value 2
Angle between veins and midrib	17° to 35° Value 0	36° to 46° Value 1	47° to 78° Value 2
Number of dentations per leaf margin	1 to 6 Value 0	7 to 11 Value 1	12 to 27 Value 2
Number of flowers per umbel	9 to 14 Value 0	15 to 20 Value 1	21 to 35 Value 2
Stiple thickness, millimeters	0.5 to 1.0 Value 0	1.5 to 2.0 Value 1	2.5 to 4.0 Value 2
Total index values	0	5	10

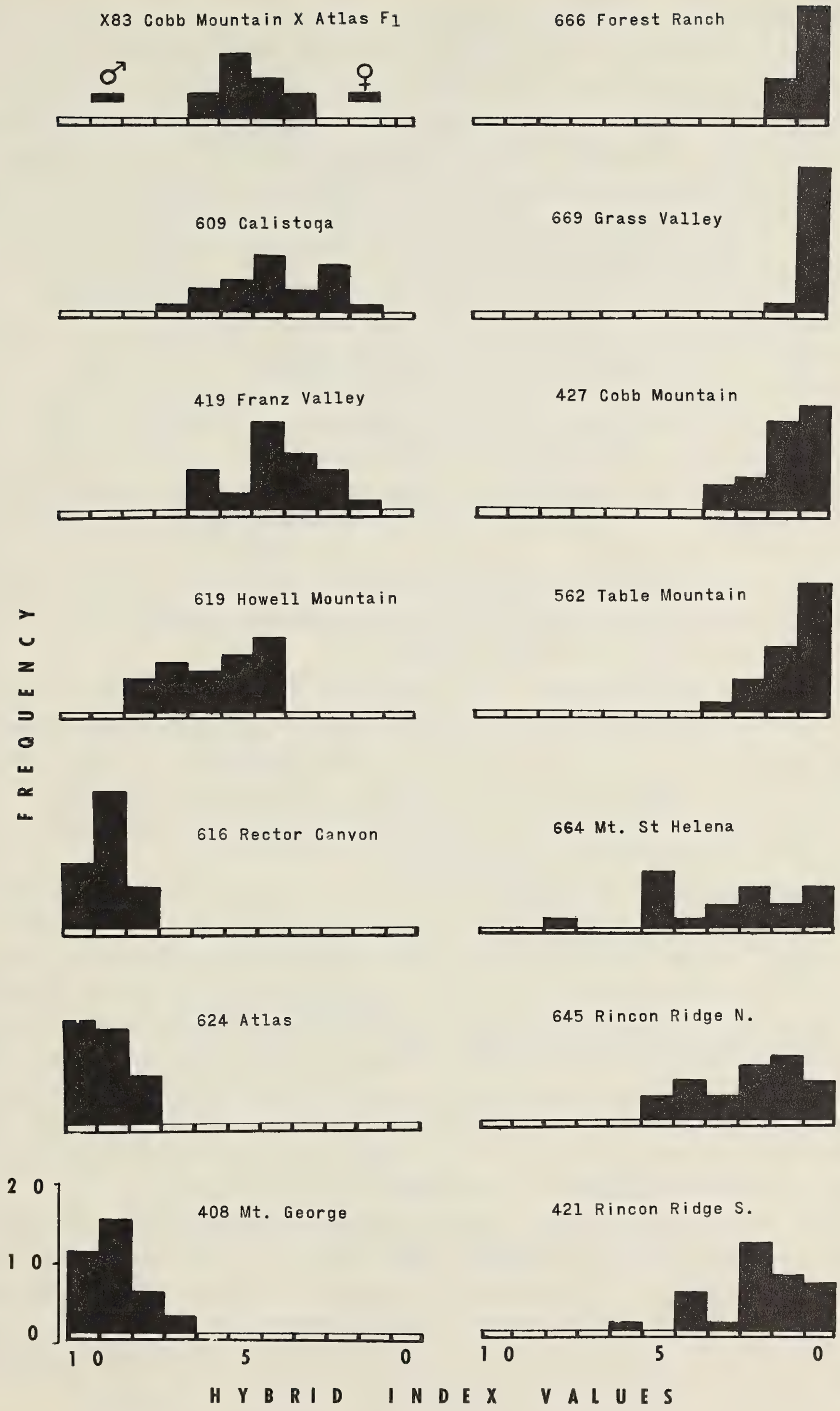


Fig. 116. Frequency distribution of index value for individuals from population samples in the C. purpureus-prostratus series. See table 13 for explanation of index values.

The typical form of *C. prostratus* from the lower Sierra Nevada is quite uniform, whereas its variety *occidentalis* varies slightly toward *C. purpureus*. *Ceanothus purpureus*, although somewhat variable throughout its range, shows a striking deviation toward *C. prostratus* at its northern limit at Howell Mountain in Napa County. The populations from the intermediate area, including *C. divergens* and *C. confusus*, are highly variable in all respects and complete this transition. The population of F_1 progeny experimentally produced from *C. prostratus* var. *occidentalis* × *C. purpureus* is definitely intermediate and closely resembles plants found in populations referred to *C. divergens*.

One population apparently of very recent origin found growing in an abandoned vineyard 6 miles east of Santa Rosa, described in detail by Howell (1940b), indicates that the broad introgressive zone between *C. gloriosus* and *C. cuneatus* meets and merges at this point with the *C. purpureus-prostratus* series. This highly complex population appears to have originated as a quadruple hybrid in which the characters of *C. cuneatus*, *C. gloriosus*, *C. purpureus*, and *C. prostratus* are recombined. It is little wonder that Howell (1940b, p. 260) should make the following statement: ''Although hybridization was thought of almost immediately as a possible cause of this series of variation, it was practically impossible at first to analyze the perplexing complex and to determine what entities might have hybridized and produced it.''

The present interpretation of this population agrees with that of Howell, who attributed the source of variation to the adjacent taxa *Ceanothus confusus* and *C. divergens* (interpreted in the present paper as of hybrid origin between *C. purpureus* × *C. prostratus* var. *occidentalis*) combined with another hybrid product between *C. gloriosus* and *C. cuneatus* (referred to in the present paper as the highly variable taxon *C. ramulosus*).

Ceanothus jepsonii. *C. jepsonii* Greene is found exclusively in serpentine soils in many localities throughout the area. It occurs in two color forms: the typical form, which has deep blue-violet flowers, is found in the outer coast range, whereas a white-flowered form, *C. jepsonii* var. *albiflorus* J. T. Howell, is found in the more arid interior ranges. Transitional populations occur in northern Sonoma and southern Mendocino counties, where the flowers are predominantly of varying shades of pale blue or pale blue-lavender; however, plants with deep blue-violet or white flowers appear also in these populations. When the plants are not in flower the two forms are nearly indistinguishable, inasmuch as they have diagnostic characters otherwise identical.

Throughout its range, this species commonly occurs adjacent to either *C. cuneatus* or *C. ramulosus*. Although these two species are genetically compatible with *C. jepsonii*, and a moderate overlap in flowering time exists among the three species (about 7 to 14 days), plants intermediate between these taxa are extremely rare. Table 14 lists the sources of the population samples and field census upon which these observations are based.

TABLE 14. Localities and Number of Individuals Represented in the Population Samples for *Ceanothus jepsonii*, *C. cuneatus*, and *C. ramulosus*

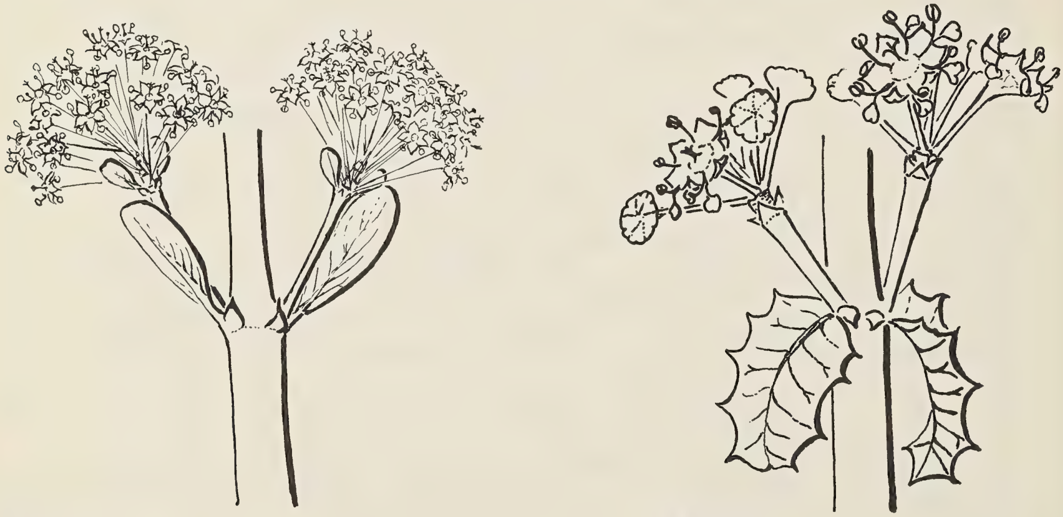
Sample Number	Number of Individuals	Source
	C. cuneatus (isolated from *C. jepsonii*)	
735	31	Cliff House, Tuoloumne Co.
458	30	Rock Creek, Nevada Co.
424	34	Howell Mt., Napa Co.
643	31	Covelo, Mendocino Co.
	C. jepsonii (isolated from *C. cuneatus*)	
563	30	White Point, Lake Co.
561	24	Mountain Mill House, Lake Co.
431	32	Mirabel Mine, Lake Co.
	C. cuneatus and *C. jepsonii* (sympatric)	
435	23 *c.*, 43 *j.*, 3 intermediates	Knoxville, Napa Co.
436	33 *c.*, 35 *j.*	Bench Mark 2012, Napa Co.
437	27 *c.*, 25 *j.*	Bench Mark 2019, Napa Co.
438	7 *c.*, 50 *j.*, 2 intermediates	McKosker Ranch, Lake Co.
439	7 *c.*, 35 *j.*	Highway 20 at Colusa-Lake Co. line
440	34 *c.*, 23 *j.*, 1 intermediate	Wilbur Springs, Colusa Co.
441	2 *c.*, 38 *j.*	Hough Springs, Lake Co.
	C. ramulosus (isolated from *C. jepsonii*)	
628	15	Mt. Tamalpais, S. W. Ridge, Marin Co.
637	24	7 miles southeast of Annapolis, Sonoma Co.
	C. jepsonii (isolated from *C. ramulosus*)	
633	29	Skaggs Springs, Sonoma Co.
	C. ramulosus and *C. jepsonii* (sympatric)	
500*	24 *r.*, 50 *j.*, 4 intermediates	Mt. Tamalpais at Bootjack Camp, Marin Co.
629-630	39 *r.*, 50 *j.*	Laurel Dell, Mt. Tamalpais, Marin Co.
631	27 *r.*, 22 *j.*, 2 intermediates	Alpine Lake, Marin Co.
401	12 *r.*, 32 *j.*	San Geronimo Ridge, Marin Co.
	Progeny of *C. jepsonii-ramulosus* intermediate 627-a x b	
X98 and 99	15	Boot Jack Camp, Marin Co. (Grown in U.C. Botanical Garden, Berkeley)

*Field census.

For comparison with the previous examples showing broad intergrading zones of hybridization, Anderson's hybrid index has again been used. The characters were chosen so that collectively they are common to both C. cuneatus and its very close introgressive derivative C. ramulosus, and could likewise be used to compare these two taxa with C. jepsonii.

Leaf characters are very useful in describing these forms. In Ceanothus jepsonii the leaves are thick, heavy, and strongly deflexed at maturity (fig. 118), whereas in both C. cuneatus and C. ramulosus the leaves are erect and plane or slightly concave (fig. 117). The leaf margins of C. jepsonii have 7 to 15 extremely prominent spinulose dentations; the margins in C. cuneatus and C. ramulosus are either entire or have a small number of inconspicuous dentations. The depth of the cusps between these dentations is conspicuous in C. jepsonii and is easily measured; these cusps contrast sharply with the shallow ones occasionally found in the other taxa. To distinguish between these two groups, the orientation of the leaf and the depth of the deepest cusp between the dentations of a characteristic leaf were used. If the leaf margins were entire, the specimen received a value of 0 for cusp character.

The inflorescence offers important diagnostic characters. Both C. cuneatus and C. ramulosus have a pair of foliar bracts on the peduncle subtending the flower umbel; in C. jepsonii these bracts are lacking. The flowers in C. jepsonii are hexamerous to octamerous and rarely exceed 10 flowers per umbel; in contrast, C. cuneatus and C. ramulosus are pentamerous, and each umbel contains a large number of flowers. The number of flower parts and the presence or



CUNEATUS

117

JEPSONII

118

Figs. 117-118. Contrasting leaf and inflorescence characters of C. cuneatus and C. jepsonii.

absence of foliar bracts from one characteristic umbel were used to contrast these inflorescence differences. These four characters are summarized with their index value in table 15, and the aggregate value for each plant in the various population samples is plotted in the histograms (fig. 119).

TABLE 15. Index Values for Four Character Differences Contrasting *Ceanothus cuneatus* and *C. ramulosus* with *C. jepsonii*

Character	*C. cuneatus* and *C. ramulosus*	Intermediate	*C. jepsonii*
Leaves	Erect Value 0	Intermediate Value 1	Strongly deflexed Value 2
Depth of leaf dentation cusp	0 to 0.5 mm Value 0	1.0 to 1.5 mm Value 1	2.0 to 4.0 mm Value 2
Inflorescence	2 per peduncle Value 0	Rudimentary and mixed Value 1	Absent Value 2
Number of flower parts	5 merous Value 0	5 to 6 mixed Value 1	6 to 8 Value 2
Total index value	0	4	8

The only highly variable intergrading population for these characters was in the artificial hybrid population, X98 and 99, grown in the University of California Botanical Garden, which was derived from mutual pollination between two plants intermediate between *C. jepsonii* and *C. ramulosus* from Bootjack Camp. *Ceanothus jepsonii*, with the exception of flower color, is highly uniform throughout its range and shows no visible evidence, either in morphology or in habitat preference, that it has incorporated characters from either *C. cuneatus* or *C. ramulosus*. Those two taxa, although highly variable in certain other respects, likewise do not show any variation in the direction of the conspicuously contrasting characters of *C. jepsonii*. The rarely found intermediate plants (1.9 per cent among the 650 individuals analyzed from sympatric populations) closely resemble the experimental F_1 hybrids.

Ceanothus jepsonii has been observed growing adjacent to only one other taxon in section *Cerastes*. On Cobb Mountain in northern Napa County, populations of blue-flowered *C. prostratus* var. *occidentalis* and the white-flowered *C. jepsonii* var. *albiflorus* meet. In the Cobb Mountain area, no intermediate plants have been found, and no morphological evidence in either population suggests genetic exchange. In the locality near Table Mountain two intermediate plants between these two taxa were discovered on the contact zone between

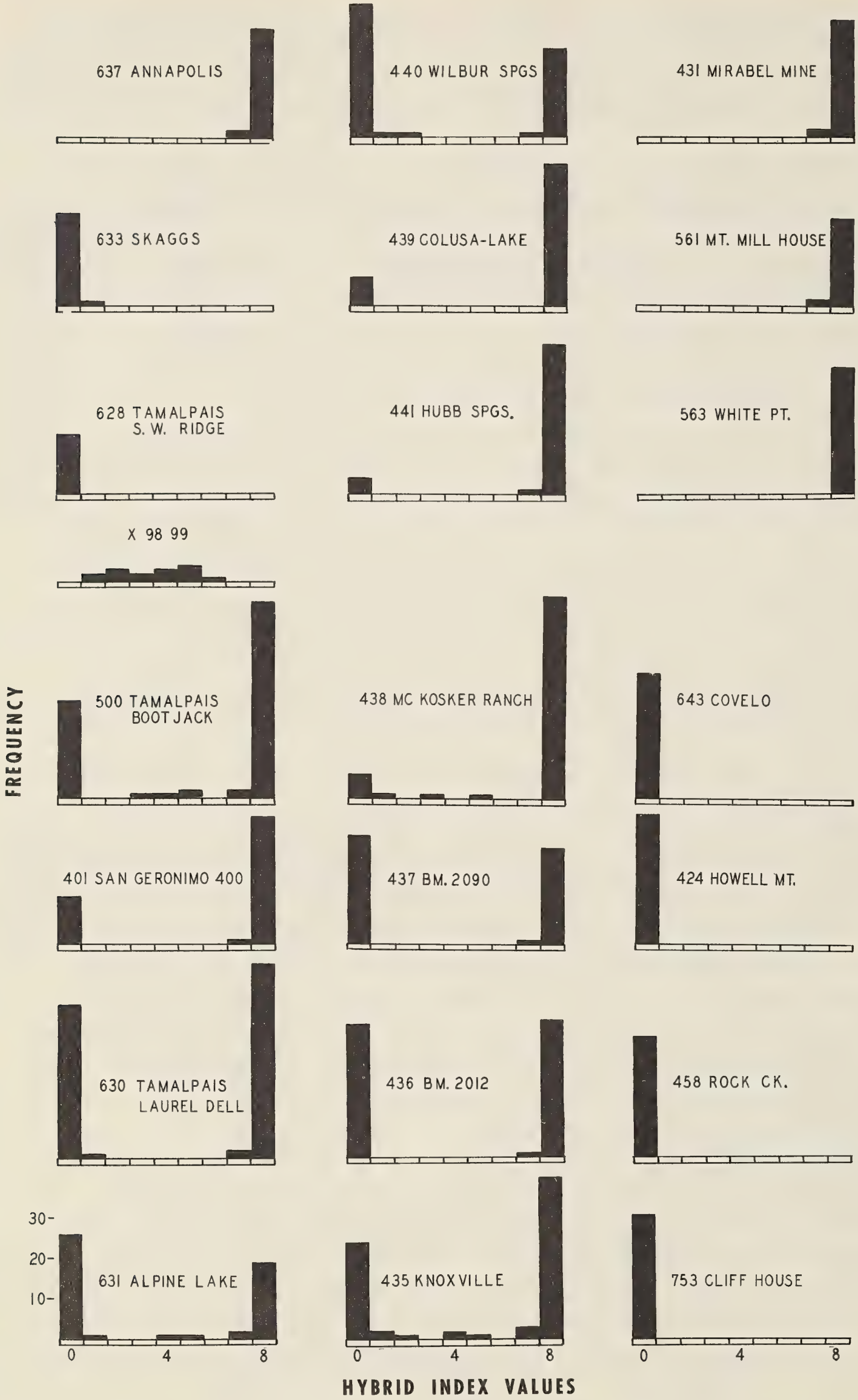


Fig. 119. Frequency distribution of index values of individuals in populations of C. cuneatus, C. ramulosus, and C. jepsonii. See table 14 for identification of the populations represented, and table 15 for explanation of index values.

serpentine and volcanics. Both had the appearance of first-generation hybrids having a suberect growing habit, intermediate leaf characters, pale blue flowers, mixed pentamerous to hexamerous flowers, and a mixed variation in the foliar inflorescence bracts. This variation included total absence of bracts, as in *C. jepsonii*, a single rudimentary bract, and two somewhat reduced bracts, as in *C. prostratus* var. *occidentalis*. Although both these plants were found to overlap the two parental taxa in flowering time, to have regular meiosis in the pollen mother cells, and to have 90 to 97 per cent stainable pollen and normal seed set, no evidence of introgression could be detected in either of the parental populations.

Ceanothus pumilus. *C. pumilus* Greene is another serpentine endemic found from the Siskiyou Mountains of southwestern Oregon south into the outer coast ranges of northwestern Sonoma County, California. Within the area included in the present study it has been found in only three localities: Red Mountain; 1 mile north of Cummings, in Mendocino County; and on the Fred MacMurray ranch in Sonoma County. In all three of these localities the populations are quite uniform, and no other representative of section *Cerastes* occurs in the vicinity. In the northern part of its range in Siskiyou and Del Norte counties of California, and in southwestern Oregon, *C. cuneatus* is commonly found growing adjacent to this species. *Ceanothus cuneatus*, as was mentioned before, is an erect shrub with entire leaves and creamy white flowers, whereas *C. pumilus* is a low decumbent to prostrate shrub with sparsely dentate leaves and intensely blue-violet flowers. *Ceanothus cuneatus*, although occasionally found on serpentinized soils, here prefers the dry, exposed metamorphic or sandstone outcroppings free of timber, whereas *C. pumilus* occurs only on serpentine soils, and usually as an understory plant in timbered areas. These two species flower simultaneously, yet where they meet in unaltered areas very few plants intermediate between the species can be found.

Under disturbed conditions, however, quite a different situation occurs. From an area of mixed parent materials in the rough floodplain of the Illinois River 3 miles north of Waldo, in Josephine County, Oregon, a population was studied that contained 22 per cent intermediates in a census of 50 plants. A similar series was collected by S. Galen Smith (S 703 and S 704) from an abandoned quarry in a serpentine contact area 2 miles east of O'Brien, Josephine County, Oregon. This series contained fourteen plants of *C. pumilus*, a series of nine intergrading intermediates, and five plants of *C. cuneatus*. Although no cytological or genetic data are available from these populations, under undisturbed natural conditions *C. pumilus*, like *C. jepsonii*, apparently fails to hybridize with other taxa growing in close proximity.

CHAPTER IV

EVOLUTIONARY PATTERNS IN CEANOTHUS

Ceanothus has been present on the Pacific slope of North America at least since the Oligocene, a period of about 36 million years. During this time profound changes have taken place in the topography and climate within this geographical area. Under these gradual but constantly changing conditions, the genus has ramified into a number of forms that at the present time can occupy environments ranging from maritime coastal bluffs to subalpine conditions, and from mesic rain forests to near-desert conditions.

The fossil record indicates that, during the Miocene, about 25 million years ago, a major divergence had occurred within the genus. At this time we have represented in the fossil record leaf forms closely resembling members of both sections Euceanothus and Cerastes. These two distinctive leaf forms are occasionally found in the same fossil floras, with no intergrading intermediate forms, a fact suggesting that at this time barriers to genic interchange may already have been developed.

Genetic differentiation between the sections. In the present-day species genetic evidence demonstrates that such barriers are present, for no genetic exchange between the sections Euceanothus and Cerastes is possible. Even though both sections have the same chromosome number ($n = 12$) and the chromosome complements are essentially indistinguishable, the rare intersectional hybrids are completely sterile. Reduction divisions in these rare hybrids show no configurations such as inversion bridges or translocation chains which would indicate that sudden major changes in chromosome repatterning in the two complements had taken place. Rather, the irregularities are represented only by a marked reduction in chromosome pairing (cf. table 6). In these hybrids about 1 per cent of the cells have complete pairing, a fact indicating that the chromosomes are homologous. A gradual accumulation of small but vital changes has apparently taken place in the germ plasm in two different directions, resulting in complete sterility barriers between the members of the sections Euceanothus and Cerastes.

Species equivalent to ecotypes within section Cerastes. The genetic pattern found between the members of section Cerastes is a direct contrast to the complete sterility barriers that exist between the sections. Hybrids between the various forms are as highly fertile as their parents. Meiosis is completely regular; seed set and pollen formation are normal; and later generations are strong and vigorous. Thus these forms, regardless of the fact that the majority are sufficiently distinct not to be questioned as species on morphological grounds, are biologically comparable to the "ecotypes" or "ecological races" of Turesson (1922) and Clausen, Keck, and Hiesey (1939 and 1940). As in the ecotype, differences in specific habitat requirements of each particular taxon not only determine their distribution but apparently also have played a fundamental role in the evolution and stabilization of their distinctive characteristics.

Genetic coherence in differentiation and stabilization of ecotypes. The genetic basis of differentiation and subsequent stabilization of ecotypes, as well as of the biosystematic units found in the members of section *Cerastes*, revolves primarily on the coherence of the genotypes balanced against the selective pressures of the natural environments. Polygenic systems that control the expression both of morphological and of physiological characters tend to be linked together through the chromosomes. Various entities that have become differentiated are thus preserved from generation to generation by this semistable genetic mechanism.

Different aspects of the principle of coherence have been followed theoretically by Anderson (1939a and b, 1948, and 1949) and by Mather (1941, 1943, and 1953), and experimentally by Clausen and Hiesey (1958 and 1960). In the last-mentioned study the operation of the principle in experimental races and hybrids of *Potentilla glandulosa* has been followed in three different environments at contrasting altitudes. It has been clearly demonstrated that characteristics distinguishing recognizable taxa from one another on the diploid level are controlled by a series of genes. In *Potentilla* the minimum number of gene pairs that interact to govern the expression of any given character distinguishing climatic races was found to range between approximately three and twenty. Such gene systems may include oppositional and hypostatic genes as well as others of simple additive type. In progeny of the second and later generations of crosses between contrasting climatic races, the expression of given characters controlled by such a series often transcends the expression of that character in either of the original parents.

Although the recombination types found in the second and later generations therefore cover a very wide range, a system of partial linkages between the genes of the parental systems tends to preserve in a majority of the second-generation progeny groups of characters typical of the two parental forms. This was found to be true not only for morphological characters but also for physiological responses. In *Potentilla* this flexible genetic system thus allows for ample release of variability among progeny after hybridization under changing environmental conditions but preserves in a semistable form combinations of characters that have proved successful in a particular environment. In stable environmental conditions, then, this coherence system under the impact of natural selection will permit two genetically compatible but distinct ecological forms to exist in adjacent but ecologically distinct habitats without losing their identity.

Dynamics of coherence in natural populations. All environments are to a certain degree unstable. Erosion, which uncovers new parent materials for soil formation, long-range changes in climate, and such events as crustal deformation, volcanism, and fire are but a few of the natural phenomena that keep the environment in a constant state of flux. The genetic systems found in *Potentilla glandulosa*, which also undoubtedly operate among the members of *Ceanothus* in the *Cerastes* section, are admirably suited to meet such changes. The various stages of differentiation in relation to habitat found in the eleven species of *Ceanothus* in the section *Cerastes* in the area north of San Francisco Bay reflect the effects of such environmental changes working on a group of plants with such a flexible genetic composition.

The majority of the species are geographically separated, and coincide in distribution with changes in ecological habitats, especially with soil type (fig. 102, p. 53). A striking exception is *C. cuneatus*, which occupies an almost continuous broad strip in the arid foothill region of the coast ranges and Sierra Nevada from Mexico into Oregon. Within the area north of San Francisco Bay, *C. cuneatus* overlaps with at least five other species belonging to section *Cerastes*, all at different places. Where the ecologic requirements of at least one of the overlapping species are strict, as, for example, in the area of the obligate serpentine endemic *C. jepsonii*, there is very little evidence of natural hybridization. In this area *C. cuneatus* is found primarily on soils derived from sandstone. Under experimental conditions the two species hybridize easily and produce highly fertile progeny. They flower at approximately the same time, and occur very close together at their zones of contact, yet in their natural environments few hybrids are found. The field studies reported above show that less than 2 per cen of the plants growing in these zones of natural contact can be identified as of hybrid origin.

Ceanothus cuneatus and *C. jepsonii* differ from each other in distinct morphological characters, and there is evidence of coherence between morphological and physiological characters that restricts them to their respective habitats. Undoubtedly natural hybridization occurs frequently, but natural selection eliminates the hybrids in competition with the parental species.

A similar condition is found where *C. jepsonii* meets *C. prostratus* var. *occidentalis*, and where *C. cuneatus* occurs with *C. pumilus*, another serpentine endemic, in Humboldt and Del Norte counties in California and in southwestern Oregon. No hybrids have been found between *C. cuneatus* and *C. pumilus* in populations of either species growing on unaltered habitats, but where the particular habitat has been changed by man's activity or other natural forces the types intermediate between these species can be as high as 30 per cent.

In southeastern Australia a group of alpine species of *Ranunculus* in section *Chrysanthe* presents another striking example of the restriction to free gene exchange between specific forms apparently evolved through strict natural selection acting in microenvironments (Briggs, 1960, 1962). The species evolved are found in the Bogong High Plains and the Mt. Kosciusko area, and include *Ranunculus millanii* F. Muell., *R. muleri* Benth., *R. dissectifolius* F. Muell. ex Benth., *R. clivicola* B. Briggs, *R. niphophilus* B. Briggs, *R. graniticola* Melville, *R. lappaceus* Sm., *R. pimpinellifolius* Hook., *R. eichleranus* B. Briggs, and *R. victoriensis* B. Briggs, all with a chromosome number of $2n = 16$.

These species are distributed in a mosaic pattern within the general area of their occurrence, each species growing in a different but strictly limited habitat as, for example, in standing water, in moist fens, or in higher, drier areas populated with tussock grasses. Contact zones between these habitats are frequent, often with only narrow and sharp transition zones between. In such transition zones natural hybrids are found, and they are strictly confined to these intermediate areas. Among the ten species involved, eighteen different spontaneous hybrid combinations have been found. The hybrids show essentially regular pairing of the chromosomes at meiosis and have normal seed and pollen.

As in *Ceanothus*, these interfertile species evidently maintain their taxonomic distinction through strict natural selection, preserving only the genetic forms that are in equilibrium with the strict demands of a narrowly defined habitat.

On a much grander scale the various species within each of the five subgenera of the genus *Eucalyptus* in Australia exhibit this same phenomenon (Pryor, 1959). The majority of the species that have been investigated cytologically have 11 pairs of chromosomes. Strong genetic barriers to interbreeding are found between the various subgenera, and species representing the different subgenera are frequently found in mixed stands in the same habitat. The species within the subgenera, on the other hand, have mostly been found to be interfertile, but each species occupies a separate kind of habitat differing in soil composition, altitude, or other features.

Where the habitat boundaries are sharp, as, for example, between different kinds of soils, only a few hybrids are found between the genetically compatible forms. These hybrids, as in *Ceanothus*, are for the most part restricted to the very narrow transition zones. The rare hybrids found in mature stands are, in these unaltered areas, inferior to the parental species occupying the same habitats and are obviously at a competitive disadvantage. Where the boundaries of the habitats between two such species are less distinct, as in the replacement of one species by another in a broad altitudinal zone, or where the habitats have been altered by clearing or burning, greater numbers of hybrid derivatives are favored.

In *Ceanothus*, likewise, where specialization of given forms for particular habitats is less highly developed, broad areas containing hybrid derivatives are found. An example is seen in the area between *C. gloriosus* and *C. cuneatus*. *Ceanothus gloriosus* is restricted to an area along the coast north of San Francisco Bay where the weather is cool and characterized by frequent heavy fogs. *Ceanothus cuneatus*, on the other hand, grows in the hot, dry inland foothills to the east. In the extremes of the two respective environments, the genetic coherence of the characteristics distinguishing the two species is apparently in equilibrium with the selective forces of the environment, and the populations of both are essentially uniform. In the intermediate zone between these two extremes, however, a highly varied series of populations is found, including forms described under the names *C. ramulosus* (Greene) McMinn, *C. sonomensis* Howell, and *C. masonii* McMinn. A statistical study of individual characters of these field populations (p. 54 to p. 63) shows that there is a continuous series of intergrades between the two extremes *C. gloriosus* and *C. cuneatus*.

Artificial hybrids between the two species segregate F_2 progeny whose characters fit in very well with the variation pattern found in natural populations of the three intermediate taxa. The evidence points strongly to the conclusion that the intermediates *C. ramulosus*, *C. sonomensis*, and *C. masonii* are aggregations of recombination products that have become semiestablished in the process of natural selection, and that new coherence equilibria between morphological and physiological attributes of *C. gloriosus* and *C. cuneatus* are currently evolving.

The intergrading series between *C. prostratus* var. *occidentalis* and *C. purpureus*, including *C. confusus* Howell and *C. divergens* Howell (pp. 64 to 72), as well as the highly variable Sierran mid-montane taxa *C. arcuatus* McMinn, *C. fresnensis* Abrams, X*C. connivens* (Greene) McMinn, and X*C. bakeri* (Greene) McMinn, which occur geographically between *C. cuneatus* and *C. prostratus* and incorporate characters from both, follow this same pattern.

Differentiation of characteristic forms can likewise be found within species that occupy a range of different habitats, as in the three varieties of *C. gloriosus*. The typical form is prostrate and confined to the exposed wind-swept ocean bluffs; the varieties *exaltatus* and *porrectus* are erect or semierect and inhabit the chaparral farther inland. The differences in growth habit between these forms are genetically fixed and are stable when the plants are transplanted to different environments or when brought into garden cultivation. Likewise *C. cuneatus* has developed innumerable recognizable forms within its extensive range, nine components of which have been recognized taxonomically. In these groups the aggregations of characters that typify each form follow essentially a clinal transition which coincides with a gradual ecological gradient similar to that found in some of the species of *Eucalyptus* in Australia (Barber, 1955; Barber and Jackson, 1957).

In *Ceanothus* of the *Cerastes* section it is apparent that constellations of characters that can be the focal points for new forms can arise in two different ways. The first is by natural selection working within the limits of a large population extending over a range of different habitats. The second is through natural selection working on recombination swarms which have resulted from hybridization between previously differentiated forms that have either been separated spatially or isolated by strict habitat requirements which have subsequently been altered as the result of environmental change. Undoubtedly an interaction of both kinds of differentiation has taken place within the section during the geological past.

Nodes of differentiation in section Cerastes. The present distribution pattern of the three crypt types in the *Cerastes* section of *Ceanothus* suggests that during the geologic past three major waves of differentiation, probably separated geographically during the period of their major development, have occurred.

The first, which includes taxa with type I crypts, appears to have differentiated along the Pacific coast and is represented at present by a series of geographically separated narrow endemics, each in a specific kind of habitat. Its range extends along a narrow coastal strip from Baja California in Mexico north into Humboldt County in California.

The second wave of differentiation appears to have been essentially northern and includes the taxa with type II crypts. With the exception of *C. crassifolius*, which is restricted to coastal southern California, the remaining products of this wave occur in the mountains from Tulare County in the Sierra Nevada northward into the Cascades of central Washington, with an arm extending southward through the Klamath and Trinity Mountains into the coast ranges just north of San Francisco Bay. These first two groups probably evolved independently under geographical isolation, the major barrier between them being the Great Valley of California, which, during the Tertiary period, was a large inland sea.

The third is the *C. cuneatus-greggii* complex with type III crypts. It appears to have had its initial differentiation toward the southeast, with a later spread into the area of the Pacific coast. Its present distribution is in the semiarid regions from southern Mexico north into Texas, Arizona, New Mexico, Utah, and Nevada, with a northwestern extension occupying nearly all the semiarid foothill areas throughout California into Oregon. This extension of the *C. cuneatus-greggii* complex in the Pacific states is of particular interest, for at present its range forms a matrix between the more restricted species of the two former groups. The active hybridization between this complex and the species of both the two former groups suggests that this invasion into California occurred later than the major differentiation of the former groups.

We are now witnessing the active development of a fourth node of differentiation. It is primarily the result of gene interchange between the *C. cuneatus-greggii* complex and the components of the two former groups under the influence of ever-changing environments. The members of these former groups under the impact of this aggressive complex, however, show no evidence of becoming submerged. Rather, a series of new forms appears to be emerging which occupy habitats different from those of their progenitors. *Ceanothus ramulosus*, *C. sonomensis*, and *C. masonii*, which occur in the northern coast regions, and *C. arcuatus* and *C. fresnensis* in the Sierra foothills, are specific examples.

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